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FRESH-WATER COPEPODA OF MASSACHUSETTS

A. S. PEARSE

IN her excellent review of the Crustacea of New England, Miss Rathbun (:05) lists nine species of fresh-water copepods for Massachusetts, as follows: —

? *Hetercope* sp.

Diaptomus leptopus Forbes.

Cyclops vernalis Fischer.

Cyclops viridis insectus Forbes.

Cyclops bicuspidatus Claus.

Cyclops albidus (Jurine).

Cyclops serrulatus Fischer.

Cyclops prasinus Fischer.

Cyclops phaleratus Koch.

As her paper cites the original description of each of these species and the authority for its occurrence in Massachusetts, these points need not be taken up here. The occurrence of *Hetercope* in America is doubtful and it cannot properly be included on the evidence that Cragin ('83) offers.

To the above list I am now able to add the following: —

Eurytemora affinis Poppe.

Epischura massachusettsensis n. sp.

? *Diaptomus ashlandi* Marsh.

Diaptomus sanguineus Forbes.

Diaptomus pygmaeus n. sp.

Diaptomus spatulocrenatus n. sp.

Cyclops edax Forbes.

Cyclops leuckarti Claus.

Cyclops viridis brevispinosus Herrick.

Cyclops fuscus (Jurine).

Cyclops bicolor Sars.

Cyclops varicans Sars.

Cyclops fimbriatus poppei Rehberg.

Canthocamptus illinoisensis Forbes.

Canthocamptus staphylinoides Pearse.

Canthocamptus northumbicus ameri-
canus Herrick.

I have also observed all the species in Miss Rathbun's list except *Heterocope* and *Cyclops prasinus*. *Eurytemora affinis* has never been observed before in America outside the Gulf of Mexico (Foster, :04). The previous eastern range of *Diaptomus ashlandi* is Indiana; *Diaptomus massachusettsensis* and *Diaptomus spatulocrenatus* are apparently new to science. The ranges of all the species of *Canthocamptus* here listed, are considerably extended. The ranges of several species of *Cyclops* are widened somewhat but this is of no very great significance as it is a cosmopolitan genus and all the species have been previously found in the United States.

My thanks are rendered to J. A. Cushman for specimens from various stations and for collections from Nantucket Island which were made by Mariana Hussey, E. W. Morgan, and S. D. Richmond. I am also indebted to I. L. Shaw for specimens from Brookline, Wellesley, and Randolph.

The types of the new species here described have been presented to the Boston Society of Natural History.

Genus EURYTEMORA Giesbrecht

Eurytemora affinis Poppe.—This species occurred in a collection from Squam Pond, Nantucket Island, made by S. D. Richmond, June 4, 1905.

Genus EPISCHURA Forbes

Epischura massachusettsensis n. sp.

This species is described from nine females collected by I. L. Shaw at Wellesley, Mass., April 20, 1905. No males were taken at that time nor in October when several dredgings were made.

Description.—Of medium size, cephalothorax elliptical seen from above, broadest about the middle, truncate at anterior end; six-segmented, first segment almost half the cephalothorax and having a suture at its middle; last segment distinct. Abdomen (Fig. 4) symmetrical, slender, five-segmented (furca included). First segment very short, second segment longest, third segment longer than first but shorter than fourth. Furca twice as long as wide, hairy on inner margin, bearing three strong plumose terminal setæ and a smaller one at both the inner (not plumose) and outer distal angles. Antennæ twenty-five-segmented and when reflexed, extending to middle of furca.

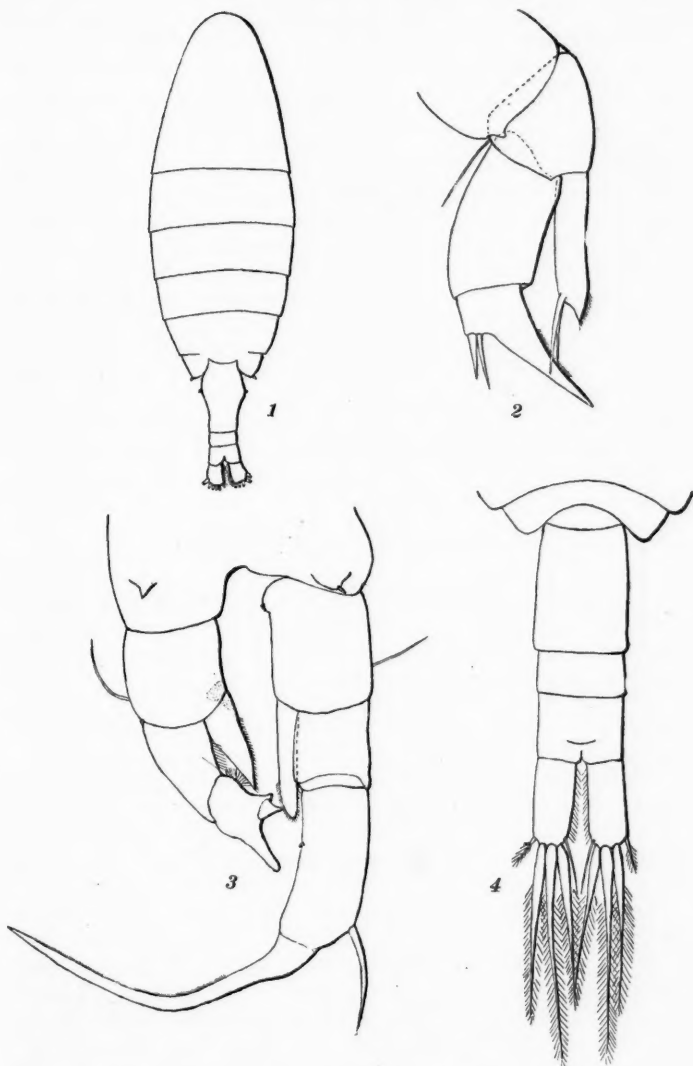


FIG. 1.—*Diaptomus pygmaeus*. Dorsal view of female. $\times 66$.
FIG. 2.—*Diaptomus pygmaeus*. Left fifth foot, female. $\times 343$.
FIG. 3.—*Diaptomus pygmaeus*. Left fifth foot, male. $\times 290$.
FIG. 4.—*Epischura massachusettsensis*. Abdomen, female. $\times 65$.

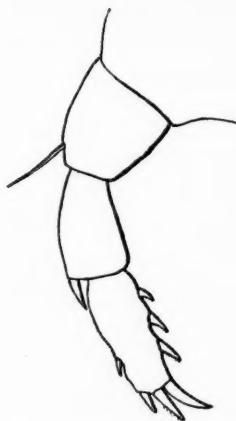


FIG. 5.—*Epischura massachusettensis*. Fifth foot, female. $\times 155$.

Fifth foot (Fig. 5) uniramose, three segmented. First segment about as broad as long, slightly tapering toward its free end; armed at outer distal angle with a slender spine. Second segment two thirds as broad as long, slightly longer than preceding segment, armed on distal end with a sharp spine at outer angle. Third segment half as broad as long and one third longer than second segment, armed on inner margin with three strong acute spines which are denticulate on the outer side; at the apex with three strong spines (middle one denticulate) the innermost of which is longest, being one third the length of the segment; on the outer margin at the distal third armed with a small strong spine.

Length of female 2.04–2.81 mm.

Genus DIAPTOMUS Westwood

? **Diaptomus ashlandi** Marsh.—A single specimen, doubtfully identified as belonging to this species, was taken at Cambridge, May 5, 1905.

Diaptomus leptopus Forbes.—This species was common from the middle of May to the middle of October. Localities: Cambridge, Medford, Wellesley.

Diaptomus sanguineus Forbes.—Collected at Wellesley and Medford in April and May.

Diaptomus pygmæus n. sp.

Figs. 1–3

Description.—A rather slender species of small size as the name indicates. The cephalothorax (Fig. 1) is widest at the middle; first segment is thrice the length of the following ones, which are about equal; last two segments are confluent above; last segment produced posteriorly and armed on each side with a short acute spine. First abdominal segment dilated laterally and armed on each side with a minute spine; second segment shorter than the third which equals the furca. The furca are two thirds as wide as long and hairy on the inner margin.

Antennae twenty-five-segmented; in the female reaching beyond tips of furcal setae and in the male to the ends of furcal rami. Male right antenna not swollen anterior to geniculate joint; antepenultimate segment without special armature.

First basal segment of right fifth foot of male (Fig. 3) slightly longer than broad and bearing a tubercle at its outer distal angle which is armed with a sharp strong spine. Second basal segment three fourths as broad as long; provided with a tubercle bearing three minute spines at the inner distal angle, and the usual hair on the outer margin. First segment of the outer ramus is as broad as long and has a ridge projecting on its caudal surface near the distal end. Second segment of the outer ramus is two and one half times as long as wide and bears a small spine on its inner margin; outer margin has a long spine more than half as long as the segment, which is placed slightly beyond the beginning of its proximal third and is denticulate on its inner margin. Terminal hook about twice as long as the preceding segment, not strongly tapering; curved somewhat sharply near the center; inner margin denticulate throughout its outer three fourths. Inner ramus of right fifth foot, one-segmented; extending well beyond the end of the first segment of the outer ramus; hairy at the distal end on both margins.

Basal segment of male left fifth foot broader than long; armed with a spinous process at its outer distal angle. Second basal segment about as broad as long; provided with the usual hair, and roughened at its inner distal angle. First segment of the outer ramus longer than preceding segment; twice as long as broad; inner surface hairy. Second segment hairy on inner proximal surface; armed with a long finger-like terminal process and also with a shorter conical process on the projecting inner surface; the latter is separated from the rest of the segment by a suture. Inner ramus one-segmented; broad at base and strongly tapering; hairy on outer two thirds of inner surface and rough on basal third; about as long as first segment of outer ramus.

First basal segment of female fifth foot (Fig. 2) produced at the outer distal angle. Second basal segment triangular and bearing the usual hair on the outer margin. First segment of outer ramus almost twice as long as wide; slightly arcuate. Terminal segment about equal to the preceding in length; slightly curved; denticulate on the middle third of its inner margin; armed on the outer side with two spines, the inner of which is one third as long as the segment and the outer one somewhat less. The inner ramus is longer than the first segment of the outer ramus; acutely pointed; hairy on inner surface at the tip; armed with two spines slightly more than one half as long as the segment.

Length: female, 1.0-1.09 mm.; male, 0.97-1.0 mm.

This species strongly resembles *D. reighardi* Marsh, but differs from it in enough points to be easily distinguished. Specimens

have been examined from Arlington, Brighton, Cambridge, and Wood's Hole, which were taken in June, July, and August. It therefore seems probable that this species is common in eastern Massachusetts during the summer months.

***Diaptomus spatulocrenatus* n. sp.**

Figs. 6-9

Description.—Cephalothorax robust and six-segmented. The first segment is three fourths the length of the cephalothorax, shows a dorsal transverse groove at about its middle. Last two segments indistinct on the dorsal surface. Last segment produced posteriorly and armed with two sharp spines on each side (Fig. 7). Abdomen stout, first segment longer than the remainder of the abdomen; second segment one sixth as long as first and one half as long as third. Furcal rami one fourth longer than wide; hairy on inner margin.

Antennae twenty-five-segmented; those of the female extending to the tips of the furca.

Right antenna of male (Fig. 6) geniculate; swollen from the eleventh segment to the geniculate joint; twelfth segment armed with a strong pointed process which is longer than the segment is wide; ninth and tenth segments armed with shorter processes; antepenultimate segment armed with a sharp curved process which is a little over half as long as the penultimate segment.

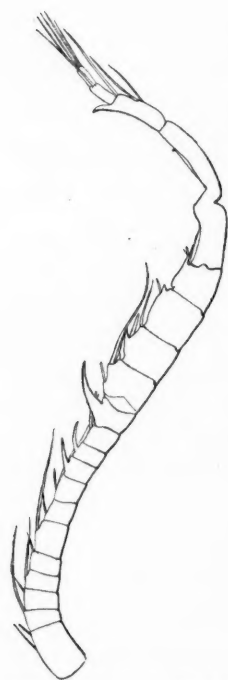


FIG. 6.—*Diaptomus spatulocrenatus*. Right antenna, male. $\times 88$.

Fifth feet of male (Fig. 8) characteristic. First basal segment of left foot reaching almost to end of first segment of outer ramus of right fifth foot; as wide as long; armed on the posterior surface with a long slender spine at the outer distal angle. Second basal segment two thirds as wide



FIG. 7.—*Diaptomus spatulocrenatus*. Left side of female showing end of cephalothorax. $\times 136$.

as long, slightly tapering, the usual hair on the outer margin. First segment of outer ramus not quite half as wide as long, hairy at the inner distal angle. Second segment hairy within, armed at the outer distal angle with a strong blunt process which is minutely denticulate on its inner margin, and at the inner distal angle with a slender hair which is as long as the segment and hairy on the inner margin. Inner ramus two-segmented, reaching almost to tip of outer ramus; first segment one fifth

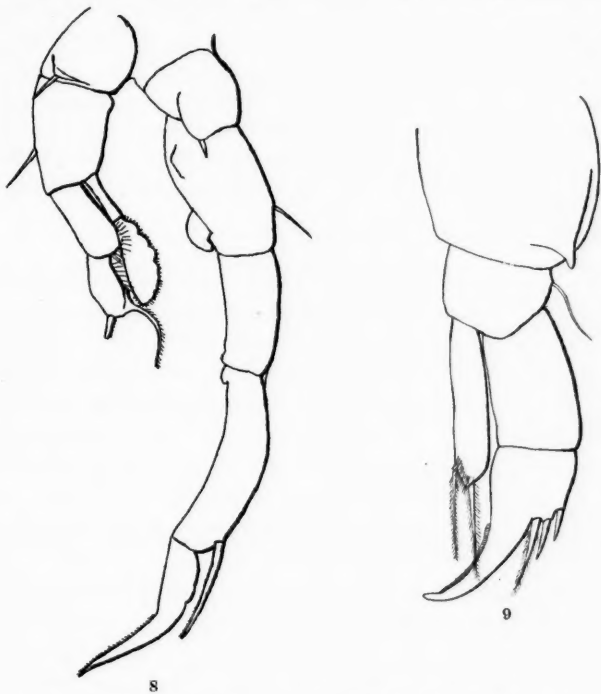


FIG. 8.—*Diaptomus spatulocrenatus*. Fifth feet, male. $\times 168$.

FIG. 9.—*Diaptomus spatulocrenatus*. Right fifth foot, female. $\times 247$.

as wide as long; second segment spatulate, crenate on inner margin, covered with minute hairs at tip and on inner and anterior surfaces. Right fifth foot of male with first basal segment armed at the distal end with a sharp spine; second basal segment armed with a large tubercle on its inner margin at the distal third and the usual hair on the outer margin. Inner ramus rudimentary being represented by a blunt curved process which does not reach beyond the end of the second basal segment. First

segment of outer ramus about as long as second basal segment, over twice as wide as long; second segment nearly twice as long as first, armed at outer distal angle with a stout hook more than one half as long as the segment. Terminal hook stout, tapering, with a sharp curve at about the middle, not quite as long as preceding segment, denticulate on inner margin beyond the sharp curve.

Fifth feet of female (Fig. 9) with the first basal segment bearing a very large pointed process at the outer distal angle; second basal segment armed with the usual marginal hair. Inner ramus one-segmented reaching beyond the first segment of outer ramus, tips hairy and armed with two plumose spines which are more than half as long as the ramus. Outer ramus two-segmented; first segment about twice as long as wide; second segment one third longer than first, curved, bluntly pointed, denticulate on outer two thirds of inner margin and armed with three spines on the outer margin of which the inner one (plumose) is longest and the outer one shortest.

Length: female, 1.47–1.58 mm.; male, 1.30–1.33 mm.

This species somewhat resembles *Diaptomus lintoni* Forbes. The specimens upon which the above description is based, were collected in Wigwam Pond, Nantucket Island, Mass., May 30, 1905, by G. D. Richmond. There were three males and two females. One of the latter was carrying eggs and both bore spermatophores.

Genus CYCLOPS O. F. Müller

Cyclops leuckarti Claus.—Localities: Cambridge, Middlesex Fells.

Cyclops edax Forbes.—Localities: Cambridge, Lexington.

Cyclops viridis insectus Forbes.—The most abundant member of this genus in the collections examined. Localities: Arlington, Cambridge, Brookline, Middlesex Fells, Nantucket, Waltham, Wood's Hole.

Cyclops viridis brevispinosus Herrick.—Localities: Cambridge, Watertown.

Cyclops vernalis Fischer.—Localities: Brookline, Arlington.

Cyclops bicuspidatus Claus.—This is a common species. Localities: Arlington, Cambridge, Middlesex Fells, Nantucket, Waltham.

Cyclops fuscus (Jurine).—Localities: Brookline, Middlesex Fells, Wellesley.

Cyclops albidus (Jurine).—An abundant species. Localities: Arlington, Brookline, Cambridge, Nantucket, Watertown, Wellesley.

Cyclops bicolor Sars.—This species was observed only once at Cambridge, on August 6, 1905.

Cyclops varicans Sars.—Occurred once in a collection made on Nantucket Island, May 30, 1905.

Cyclops serrulatus Fischer.—An abundant species. Localities: Arlington, Brookline, Cambridge, Middlesex Fells, Nantucket, Randolph, Watertown, Wellesley.

Cyclops phaleratus Koch.—Localities: Cambridge, Wellesley.

Cyclops fimbriatus poppei Rehberg.—Localities: Cambridge, Middlesex Fells, Nantucket.

Genus CANTHOCAMPTUS Westwood

Canthocamptus staphylinoides Pearse.—This is an abundant species. Localities: Cambridge, Middlesex Fells, Nantucket, Reading, Wellesley.

Canthocamptus illinoisensis Forbes.—Common in a dredging made October 9, 1905, at Wellesley.

Canthocamptus minutus Claus.—Localities: Middlesex Fells, Stony Brook.

Canthocamptus northumbicus americanus Herrick.—This species occurred in a collection made October 9, 1905, at Wellesley. The length of the female was 1.16 mm. which is longer than Herrick ('95) gives. In other respects the female was similar to his figures in Plate 29. No males were taken.

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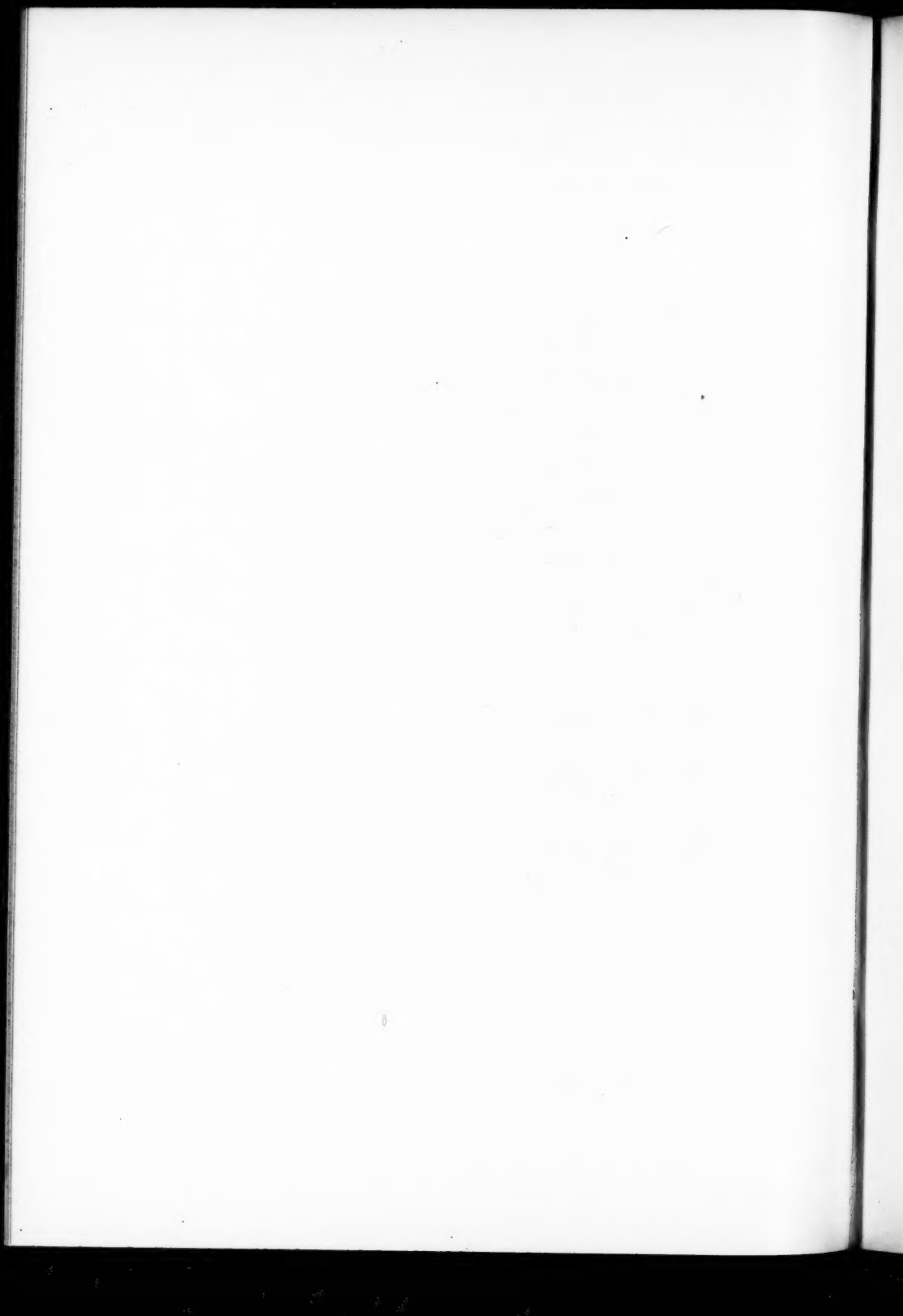
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VARIATIONS IN THE POLLEN GRAIN OF *PICEA EXCELSA*¹

JAMES B. POLLOCK

INTRODUCTION

WHILE teaching the reproduction of gymnosperms to a class in the University of Michigan, the writer observed a very unusual structure in a pollen grain of *Picea excelsa* L. (Pl. 1, Fig. 10). The structure of this pollen grain was reported at the meeting of the Botanists of the Central States, in December, 1901, and the suggestion was made that possibly the extra cells found at the dorsal side of the pollen grain should be interpreted as a prothallium, much more highly developed than usual.

On using some of the same material for other classes it was found that the structure in question occurred rather frequently, along with other variations in the structure of the pollen grain of *Picea*, so that it was considered of sufficient importance to report in the present paper. As will appear later, a further examination of numerous pollen grains has led to an interpretation of the observation different from the one suggested above.

The material was a part of the stock material of the botanical laboratory at the University of Michigan, collected May 14, 1884, but there was no indication on the label as to who was the collector, where it was collected, or of the method of killing the material. The condition of the material suggested that it was killed by putting it directly into alcohol. In all the grains the protoplasm was considerably contracted from the walls of the cells, but was otherwise well preserved.

METHODS

In order to make the interior structure of the pollen grains as plain as possible, the anthers, which were almost at the stage of

¹Contribution 88 from the Botanical Department of the University of Michigan.

dehiscence, were allowed to stand in a solution of Kleinenberg's hæmatoxylin for twenty-four hours. They were then washed in alcohol and changed very gradually from 96% alcohol to pure clove oil. In the clove oil the pollen sacs were broken up and the pollen grains set free in the oil. The pollen grains were studied by mounting a drop of the oil containing them. It was found that the pollen grains stained very unequally, some not having stained at all, and others having stained so densely that the interior could not be seen. Examination showed that the unstained ones were often the most satisfactory objects for study, so no further efforts at staining were made. This is the method used in demonstrating the interior structure of the pollen grain to large classes, and the author has no claim as the originator of the method. When the grain is thoroughly permeated by the clove oil it becomes so transparent that the interior can be seen very plainly.

The contracted condition of the protoplasm of the various cells in the interior of the pollen grain made the outlines of these cells very plain, and their number easy to determine with certainty in a large series of the grains examined. Thus the crudeness of the method of killing the material proved a decided advantage in the study of it. Another advantage appeared in mounting the pollen grains in clove oil, in that the same individual pollen grain could be studied from different points of view on causing it to roll over by means of pressure on the cover glass. Two views of the same pollen grain are shown in Figs. 11 and 12, also in Figs. 13 and 14 (Pl. 1).

HISTORICAL

The older literature concerning the pollen grain has reference to the external characters and structure, and for the internal structure there is no need to go farther back than 1834, when von Mohl published his work, *Ueber den Bau und die Formen der Pollenkörner* ('34). In this article von Mohl cites the older literature on the subject, and figures pollen grains of a few gymnosperms. His figures, however, do not show internal structure, and only in the work of Fritzsche (1836), do we first find figures which show something of the internal structure of the pollen of gymnosperms as we now know it.

Among numerous species of angiosperms and a few gymnosperms Fritzsche ('36, p. 693) described and figured the pollen grains of *Pinus sylvestris* and *Pinus larix* (*Larix europæa*). The terms he used for the different cells formed in the pollen grains were totally different from those now in use. He did not regard the bodies seen as cells, nor did he have any knowledge of their function or homology. His figures show, however, a remarkable accuracy of observation, if we take into consideration the state of knowledge of his time, and the comparatively poor microscopes and crude microscopical methods. He examined the pollen grains in oil of lemon (Citronenöl), and he undoubtedly saw one of the disintegrating prothallial cells in both *Pinus sylvestris* and *Larix europæa*. His Plate 3, Figure 10, shows this for the former, and Figure 14 for the latter. In *Larix*, besides the disintegrating prothallial cell, he showed the cells which were later called the "stalk" and "body" cells. The latter, Fritzsche called the central vesicle, and the other two cells he called "Zwischenkörper."

Later investigations have shown that in *Larix*, and sometimes in *Pinus* also, there are two prothallial cells cut off which later may disintegrate wholly or partly. It is not safe, however, to conclude that these genera vary in the number of prothallial cells formed merely because Fritzsche did not see two of them while other writers have done so. When we remember the difficulties encountered by later observers equipped with much better microscopes than Fritzsche could have had in 1836, the wonder is that he saw so much.

Meyen ('39) pointed out that Fritzsche's "Zwischenkörper" were really cells, and that one of them served as stalk of attachment to the larger cell. This was probably the first application of the term "stalk" to this cell ('39, p. 189).

For about two decades after this time the literature concerning the pollen grain is occupied mostly with evidence for and against the view of Schleiden, advanced in 1837, that the embryo has its origin in the pollen tube. Schacht ('52, p. 407) went so far as to say that the pollen is the egg of the plants, and that there is no real analogy between animal and plant fertilization among phanerogams.

Hugo von Mohl ('55), Hofmeister ('55), and others opposed

these views, and it was only when Schacht himself discovered in *Gladiolus segetum* ('58a) a case in which the embryo undoubtedly originated in a cell which was in the embryo-sac previous to the advent of the pollen tube, that the controversy practically came to an end in favor of the views of Hofmeister and von Mohl.

Schacht ('60) reported variations in the structure of the pollen grains of several gymnosperms. On page 143 of the article designated he says that the pollen of *Cupressus sempervirens* has a slightly elongated roundish form, which has divided into two unequal cells when the anther opens. *Thuja orientalis* shows the same relation, only here *oftener than in Cupressus* (italics are mine) further division takes place in the larger cell. Two of these extra divisions are shown in his Figures 22 and 23, Plate 17. The text cited above implies that similar divisions are formed in *Cupressus*, but none are figured. Schacht also found variations in the number of cells in pollen grains of *Larix europæa*, shown in his Figures 4 and 5. Since Schacht did not understand that one or more of the cells first cut off in these pollen grains may disintegrate, it is possible that his observations do not really mean a variation in the total number of cells formed in *Larix*, but his figures seem to the writer to indicate that he actually observed such a variation in *Larix europæa*. He also states ('60, p. 144) that *Abies pectinata* (Tanne), *Picea vulgaris* (Fichte) [*Picea excelsa* L.], and *Pinus sylvestris* (Kiefer) are like *Larix* in the interior of the pollen grain, only in the first two there are almost always three cells, and in the latter sometimes only two. No figures are given for these, but it seems probable that Schacht really observed variations in the number of cells in the pollen of the species named. Schacht was probably the first to figure the sperm cells ('58a) though he did not understand their function.

Hofmeister ('62, p. 406) described the structure in the pollen of *Juniperus*, *Taxus*, and *Thuja* differently from what it is now understood to be, but the apparent variation is probably due to a wrong interpretation.

Juranyi in a preliminary notice in 1870 and in the fuller article in 1872, reported a variation in the number of cells found in the pollen of *Ceratozamia longifolia* Miq. He found that the one-celled stage of the pollen grain divided into a large and a small

cell, the latter bulging into the former. The smaller cell divides again into two unequal cells, the smaller lying against the pollen grain wall, the larger one being hemispherical. Most pollen grains are ripe at this stage of development, and undergo no further changes till the time of fertilization. Often, however, one meets a pollen grain which does not remain at this stage of development, but goes a step farther in that the hemispherical cell divides once more, so that a three-celled body is found in the interior of the pollen grain. Juranyi's Figures 3 and 8 of Plate 33 ('72) show very well what he found. He, as well as Hofmeister, was mistaken as to the divisions of the smaller cells, since later investigations have shown that the small cells are cut off successively from the larger one and that only the last of the smaller cells divides when the "stalk" and "body or central" cells are formed. Juranyi's figure ('72, Pl. 33, Fig. 8), which shows three small cells, may either be an actual variation in the number of cells, or it may be a case of premature division into "stalk" and "central" cells. No certain conclusion can be reached, but if the division into "stalk" and "central" cells is the same in *Ceratozamia* as Webber found in *Zamia*, then Juranyi's figures of the former do indicate a variation in the number of prothallial cells or else a two-celled stalk. In 1882, Juranyi reported that he had seen a few cases among the *Cycadaceæ* in which the small cells could divide parallel to the long axis of the prothallium (*Vorkeim*), and that in *Larix europæa* he found some pollen grains in which the prothallium ended with two cells lying beside each other, and separated by a division wall. The upper cell had divided parallel to the long axis of the prothallium. In the cases just mentioned in which the small cells in some of the *Cycadaceæ* divide parallel to the long axis of the prothallium, it cannot be questioned that we have a case of variation from the normal, both as to the number of cells formed, and as to the relation of those cells to each other in space. In the cases of *Larix europæa* in the upper cell there may have been an earlier division than usual into the two sperm cells, though at the time these observations were made the exact origin of the sperm cells was not understood.

Strasburger, in *Die Coniferen und Gnetaceen* ('72) added much to our knowledge of these plants, though some of his observations

were inaccurate and his earlier conclusions wrong. Strasburger wrongly interpreted the disintegrating cells at the base of the pollen grain as mere slits in the wall having an origin similar to that of the wings of the grain ('72, p. 127). Schacht ('60) had interpreted these correctly as also had Meyen ('39). Following Hofmeister's suggestion Strasburger said that the cells formed in the interior of the pollen grain could only be considered vegetative cells, homologous to the prothallium of the fern. He supposed the large cell of the pollen grain corresponded to an antheridium, believing that it furnished the male gametes. He also thought that the cell structure was the same in *Pinus*, *Podocarpus*, and *Cupressus* ('72, p. 130). Later investigations have shown that no two of these are *exactly* alike. On page 131 Strasburger ('72) remarks that the number of cells which are formed by division in the pollen grain in Cycads and Coniferae remains constant. It never exceeds two, according to his observations. The report of a larger number can only be founded on the view that the split in the wall is a disintegrated cell.

In a paper published in 1875, Tschistiakoff wrote that where there are several small cells, they arise *by successive division of the large pollen cell* as in *Larix*, or the second cell can divide to form two cells as in *Ginkgo* ('75, p. 100). In *Pinus* according to Tschistiakoff two, or at the most three small cells arise. The one or two first cells arise by a real division of the large pollen cell. The small cells may have their whole volume in the intine. The third large cell, arching into the pollen grain, arises by division of a small cell. In *Abies* the third cell forms by free cell formation, this divides into two, each of these can divide again, and these secondary cells can divide longitudinally or transversely. The small cells (Suspensorzellen) can likewise divide.

Though some of the observations made by Tschistiakoff were inaccurate, at least two new truths were presented, even if they were not proved, namely, that several small cells were cut off successively from the large pollen cell in such grains as those of *Larix* and *Pinus*, and that the last one of the row of cells formed, became the progenitor of spermatozoid mother cells. His article also mentions variations in the prothallium of *Abies*, and in the number of cells formed in *Thuja*, where he says there may be two divisions instead of one, and these may be in different directions.

Both of the two truths presented by Tschistiakoff were either denied or ignored by later writers, (Strasburger, '78; '80). While Juranyi ('82) admitted Tschistiakoff's view of the origin of the small cells, proving it in Cycads, and believing it true for Coniferae, both Juranyi and Strasburger believed the large tube cell of the pollen grain furnished the male gametes and therefore represented an antheridium, and it was not until Belajeff ('91-'93) proved the contrary for *Taxus baccata* that the correct view was finally established, and generally accepted. Both Belajeff ('91-'93) and Strasburger ('92) showed that in the Abietineae also it was not the tube cell, but the end cell of the row of interior cells formed, from which the male gametes were derived. Strasburger ('84) had previously admitted that Tschistiakoff's view of the origin of the small cells in the pollen was correct, and he had also shown that in *Larix europæa* the third small cell cut off from the large pollen cell divided into two cells which he named the "stalk" (see Meyen, '39, p. 189) and "body" cells respectively. The recognition of the "splits" in the wall of *Larix* pollen as disintegrating cells ('84, pp. 2-3) was a confirmation of the earlier views of Schacht and Meyen.

Strasburger ('92) reported some interesting variations in the number and arrangement of cells in the pollen of *Ginkgo biloba*. Ordinarily there are three narrow cells and one large one found in the ripe pollen grain. Usually the first two of the former are disorganized, but it often happens that two prothallium cells are absorbed and yet two permanent ones are found. Also pollen grains were repeatedly observed in which there were three permanent inner cells preceded by one absorbed cell. Finally one grain was seen in which all three prothallium cells were permanent, and the first of these was divided longitudinally. Also (Strasburger, '92, p. 18) the stalk cell of the antheridium appears to divide under some circumstances.

Since 1893 the most important step in the progress of our knowledge of the pollen of gymnosperms was the discovery of motile spermatozoids in 1896 and 1897, by Ikeno ('98) in *Cycas*, by Hirase ('97) in *Ginkgo*, and by Webber ('97) in *Zamia*. Webber's (:01) observations on *Zamia* and *Ginkgo* are interesting from the point of view of variation in those genera. He did not work out

the details of the formation of prothallial cells, but in the species of *Zamia* studied there were always at least two prothallial cells cut off at one side and projecting into the grain as in *Ceratozamia* and *Macrozamia*, and different from *Cycas* and *Ginkgo*, where the walls are straight across the grain and not arching into it. It seemed to Webber, however, that three prothallial cells were occasionally formed, and in this case the first one was resorbed as described by Strasburger and others in *Pinus*, *Ginkgo*, etc., remaining as a dark refractive layer in the wall of the pollen grain, situated at the point of contact of the other cells. In many instances in mature grains, and in later stages, during germination, no indication of this resorbed prothallial cell can be observed, but in some cases it is unmistakable. A careful investigation of the development of the pollen in *Zamia* will have to be made before it can be determined whether three prothallial cells are regularly formed or whether the remnants of a third cell, occasionally observed, are to be considered as cases of rare and somewhat abnormal development.

Webber (:01, p. 24) clears up a point in the origin of the stalk cell and the central cell (body cell of Strasburger) showing that they originate by the division of the inner prothallial cell. Up to the time of Webber's full publication this point was quite obscure and this brings it in agreement with the facts in other gymnosperms investigated, except that the sterile cell bulges strongly into the stalk cell and this had led to a wrong interpretation. Webber also shows that *Ginkgo* is *probably* similar to *Zamia* on this point, and Seward and Gowan (:00, p. 130) show that this is actually the case. They also state that in *Ginkgo* the pollen grain at maturity contains a prothallium of from 3 to 5 cells.

Lang ('97) reports that *Stangeria paradoxa* has two prothallial cells when pollen is shed, but his Figure 18, Plate 22, seems to show three.

An interesting question is suggested by the different results observed in two species of the genus *Ephedra*. Jaccard ('93) reported that in *E. helvetica* at the time of anthesis there were in the pollen grain three free nuclei, but not separate cells, and he called these nuclei respectively the prothallium nucleus, the generative nucleus, and the tube nucleus. Land (:04) in *Ephedra*

trifurca found two persistent prothallial cells, the first cut off by a wall, the second not so cut off, while a third cell which he calls the primary spermatogenous cell divides into the stalk and body cells, which are not separated by a wall, but have a common membrane (not cellulose but plasmic?). At time of anthesis therefore it has two prothallial cells, a stalk cell, a body cell, and a tube nucleus. Land (:04, p. 8) remarks that it is hardly to be expected that two prothallial cells will be present in one species and wholly absent in another of the same genus. The question, however, cannot be settled in this summary manner. Jaccard's observations can be set aside only after further examination of the same species he studied, and not by the examination of another species.

Miss Ferguson (:01, Pl. 12, Fig. 6) figures pollen grains of *Pinus strobus* with two prothallial cells, and also with one prothallial cell (Pl. 12, Fig. 8), and in the latter case she labels the one cell shown as the *second* prothallial cell. Of course this is on the supposition that the same number of cells is always produced in this species, and that in the pollen grain shown in her Figure 8 the first cell formed had disappeared. The question naturally arises, however, whether this may not be a real variation, and the prothallial cell shown, be the only one formed in this case. A decisive answer of course must rest on further observations.

Coker (:02) has described some interesting variations in *Podocarpus*. The two prothallial cells do not promptly disintegrate, but persist as cells, and the second, and sometimes the first also, behaves in a manner hitherto unknown among the Conifers, and only paralleled among the Cycads and in Ginkgo. The nuclei enlarge and become as conspicuous as the generative nucleus. The cytoplasm of the second prothallial cell loses its individuality and its nucleus slips from its former position and lies free in the general cytoplasm. This nucleus may divide amitotically before liberation. In such cases the two nuclei generally slip out in different directions and place themselves on opposite sides of the generative cell (Coker, :02, Pl. 5, Figs. 8, 10). The number of cases in which this division occurs is probably as great as the number in which it does not occur. Hundreds of cases were found. In not a few cases the first prothallial cell liberates its nucleus into the general cytoplasm.

Arnoldi (:00) has reported a variation somewhat similar to this in *Cephalotaxus fortunei*, where he found the *tube nucleus* dividing amitotically, thus showing three free nuclei in the end of the pollen tube besides the generative cells. Arnoldi actually observed one case of division of the tube nucleus. He also reports that the non-functional male nucleus may divide amitotically in the upper part of the egg. Two tube nuclei were reported by Juranyi ('72, Pl. 34, Figs. 11, 12) in *Ceratozamia*. Two or more tube nuclei have been reported in the angiosperms, (Chamberlain, '97; Fullmer, '99; Smith, '98). The last-named author found two tube nuclei in half the pollen grains examined in *Eichhornia crassipes*.

Juel (:04) has found in *Cupressus* a variation which he seems to have discovered for the first time among the gymnosperms. In the pollen tube of this genus he found not merely two sperms, but from eight to ten, or even twenty in some cases. Chamberlain ('97) had found in angiosperms occasionally a pollen grain with three sperm nuclei. In the same species, *Lilium philadelphicum*, he also found a number of cases of a prothallial cell cut off at one side of the pollen grain.

Thompson (:05) has reported that in the pollen tube of *Araucaria* and *Agathis* there are supernumerary nuclei. His preliminary note did not disclose their origin.

Lopriori (:05) shows that in *Araucaria bidwellii* these supernumerary nuclei arise from cells formed in the pollen grain, primarily by unequal division of the large cell of the pollen grain, and the smaller cells thus cut off may themselves divide until there are fifteen or more. These cells at first have walls but the walls dissolve and the nuclei come to lie free in the pollen tube. Lopriori believes these cells are spermatogenous cells and the nuclei derived from them male nuclei. The writer does not accept this interpretation of Lopriori and will give reasons for his opinion in connection with a later discussion.

Miyake (:03) found in *Abies balsamea* that the second sperm nucleus, the tube nucleus, and the stalk nucleus which are left in the upper part of the egg after fertilization, may all divide, or attempt to divide, before they disintegrate. He says that the division figures are more or less abortive or abnormal, hence the divisions are apparently mitotic ones. This author saw one case

of "double fertilization," in which the second sperm nucleus united with a secondary segmentation nucleus of the fertilized egg.

If one could always rely on the observations reported in the literature, the conclusion would have to be drawn that in other gymnosperms than *Cupressus* and possibly the *Araucarineae* there were variations in the number of male cells. Tschistiakoff supposed that there might be numerous spermatozoid mother cells formed and Strasburger ('80, p. 49) writing of *Juniperus virginiana* states that one of the two primordial cells found at the tip of the pollen tube, divides into two, and often into two more, and these are used for fertilization. At a later date, however, the same author states ('92, p. 32) that in all the cases he has had opportunity to study exactly, the generative (primordial) cell of gymnosperms divides into two sister cells. Both are generative and even in the *Cupressineae* both are called to perform a sexual function (p. 33). In the *Abietineae* a difference in size between the cells makes its appearance, and finally in *Taxus* a very unequal division of the generative cell takes place, and only the larger sister cell functions in fertilization. Since that statement was written by Strasburger, numerous writers all report only two male cells from each pollen grain, and we must conclude that the earlier observations were not correct as to the larger number; so that *Cupressus* stands alone among the gymnosperms in forming numerous sperm cells, unless the supernumerary nuclei reported in the pollen tube of *Araucarineae* by Thompson (:05) and Lopriori should prove to be sperm cells, as Lopriori believes or else this variation among the gymnosperms has been generally overlooked. The variation in the *size* of the male cells formed is common.

In a recent work on the gymnosperms, in fact the only one in which an adequate discussion of the group is given from the modern point of view (Coulter and Chamberlain, :03) a variation is noted in the *Cycadaceae* and *Ginkgo*, as compared with other gymnosperms, in the relative position of the "stalk" and "body" cells. They are said to stand side by side, instead of dorsiventrally as they do in the other gymnosperms. These descriptions (pp. 25, 42) are evidently based on the descriptions and figures of Hirase for *Ginkgo*, and of Ikeno for *Cycas*. If Webber's completed

work on *Zamia* (:01) had appeared somewhat sooner the descriptions as to *Ginkgo* would necessarily have been different in the above-mentioned work. Webber shows very conclusively that in *Zamia*, and in all probability in *Ginkgo* also, the division into stalk and central cell (body cell) does not leave those cells side by side, but in the position found in the other groups of gymnosperms. The bulging of the last vegetative prothallial cell into the stalk cell probably led to a wrong interpretation of the earlier observations. Webber pointed out that the work of Ikeno and Hirase was obscure on this point, and that before it can be certainly concluded that any Cycad divides so as to bring the stalk and body cell side by side, except as an unusual variation, the figures showing the stages of development must be more convincing than those now available.

Lawson (:04) found a variation in the behavior of the nuclei and cells in the pollen grain of *Cryptomeria japonica*, as compared with other gymnosperms which have the same number of nuclei. The primary spermatogenous nucleus is free in the cytoplasm of the pollen grain and not separated from the tube nucleus by any membrane, except for a short time, and even then the membrane is so difficult to distinguish that it almost escaped the observation of the author.

Variations in the pollen grain of several gymnosperms have been reported in the *Botanical Gazette* by Coker (:04a) one of which is much like some of those found in *Picea excelsa* by the present writer. Coker's Figure 7 of *Larix europæa* is similar to my Figure 8. His Figure 6 is merely an earlier stage of the same thing. His Figure 8 of *Larix europæa* and Figure 4 of *Cupressus sempervirens* show a condition that is like that found by Lawson in *Cryptomeria japonica*. Coker's Figure 9 of *Larix europæa* shows the last division wall in the pollen grain straight across, as is usual in *Cycas*, instead of the strongly bulging wall that is usual in *Larix*.

Coker merely reports these as abnormal grains, apparently not attaching any significance to them. It seems to the writer that they are of some significance, at least as indicating the limits of variation in the different genera and species of gymnosperms, and when our knowledge of these variations is more complete they may be of some assistance in determining whether or not the struc-

ture of the pollen grain in gymnosperms is at the present time in a state of stable equilibrium or in a process of retrogressive modification. Coker's Figures 6 and 7 will be further noticed in connection with some of mine.

PICEA EXCELSA

In presenting my own observations I have considered it desirable to illustrate rather fully the different variations found in the pollen grains of *Picea excelsa* L., and these illustrations show a surprising range in the variation in internal structure of the pollen. One fact that seemed especially significant was that so few pollen grains could be found showing satisfactorily what has been called the "normal" structure, that is showing *two* disintegrating prothallial cells. For the larger number of pollen grains showed only one such disintegrating cell without a trace of a second, even as a split in the wall of the pollen grain. In order to get at the proportion of those which showed only one disintegrating prothallial cell, 466 pollen grains were counted. Only those were counted which lay in the position most favorable to the necessary observation, that is, the side view as shown in Figs. 1-6 (Pl. 1). No pollen grain was counted unless its internal structure seemed reasonably clear. Of the total of 466 grains counted, 310 or 66.5% showed only one disintegrating prothallial cell with no trace of another even as a split in the wall; 73 or 15.7% showed more or less plainly two disintegrating prothallial cells; 18 or 3.8% showed no disintegrating cells; 65 or 13.9% were doubtful as to whether they had one or two disintegrating cells. Even if all the doubtful ones are counted as "normal" the percentage of those grains which showed only one prothallial cell is still more than twice as great as the "normal." Of course it may be said that in those grains in which only one prothallial cell showed, the one first formed had completely disappeared. But if it is not to be seen, what evidence is there that it was ever formed? Two reasons may perhaps be given for believing in its formation and disappearance. First, in many cases in which two prothallial cells may be recognized the one first formed is barely recognizable as a mere slit in the wall of the pollen grain, and it is probable that in some cases the cell

disappears so completely as not to be recognizable at all. Second, it is said that the pollen grain of *Picea* always forms "normally" two prothallial cells which disintegrate more or less, hence when only one is found the other must have disappeared. Some validity must of course be granted to the first reason given. It is probably true in some cases, but it is absolutely impossible to prove its truth in a given case, hence the number of cases in which it is true is purely a matter of conjecture. As to the second reason given, it is a conclusion based on observation, and cannot be used to prove the correctness of the observations upon which it rests. Back of it lies the assumption that the "normal" is invariable, an assumption which is far from the truth. Even if some pollen grains of *Picea* have been shown to form two disintegrating prothallial cells, it does not at all follow that they do so invariably.

Fig. 4 (Pl. 1) shows a pollen grain in which there were undoubtedly *three* disintegrating prothallial cells. All of them were persistent, and separate from each other, and from the antheridium part of the pollen grain, so that there was no difficulty in recognizing the number certainly. This grain was at the stage preceding the division which separates the stalk and the central cell. The third disintegrating cell cannot be interpreted as a stalk cell, first, because it so closely resembles the other disintegrating prothallial cells in size and appearance, and second, because it is so completely separated from the dome-shaped cell to which it would be closely attached if it were a stalk cell.

Fig. 5 (Pl. 1) shows a variation in the *position* of the prothallial cells, though their *number* is "normal," that is, two. In Fig. 6 (Pl. 1) there is a variation in both the number and the position. Three pollen grains were seen like Fig. 5, but only one like Fig. 6. The latter shows without any doubt whatever a case of three prothallial cells in addition to the stalk cell, central cell, and large cell that forms the pollen tube. If Fig. 4 has been correctly interpreted, it and Fig. 6 furnish direct proof that the number of prothallial cells in *Picea* may vary from what has been called the normal in the direction of a greater number and it seems much more probable that they would also vary in the direction of a smaller number, since so many of the gymnosperms, as *Thuja* and *Juniperus*, have no vegetative prothallial cell.

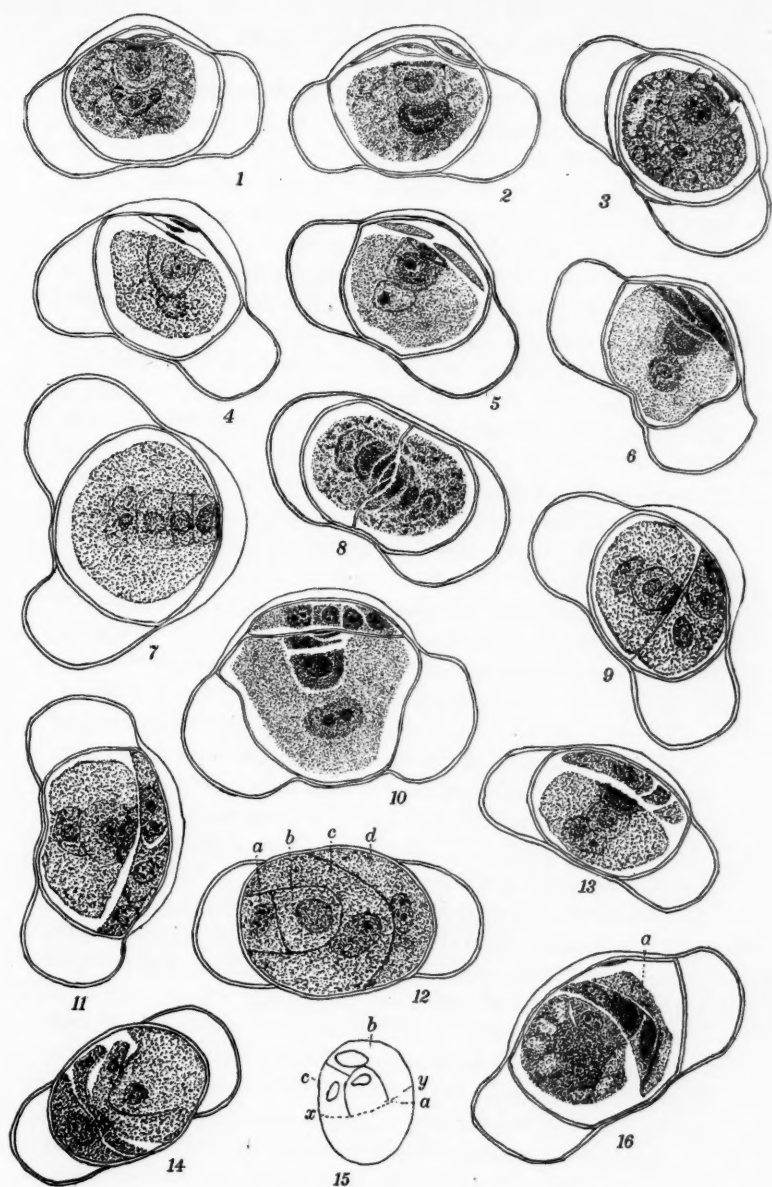


PLATE I.
Picea excelsa, variation in the pollen grains.

Fig. 2 (Pl. 1) also seems to show three prothallial cells, one with no protoplasm, and two with very little. In this case the walls of the cells had persisted after the protoplasm had almost or entirely disappeared, and so far as appearance was concerned seemed to be like the inner layer of the pollen grain wall and continuous with it. Usually, however, these cells do not show so persistent and evident a membrane. Fig. 1 has the number regarded as the normal for *Picea*. In this case also the membrane persisted after the protoplasm was entirely gone in the first one formed, showing that the membranes were not plasmic, but in all probability of cellulose. No microchemical tests were made on them. Fig. 1 shows a distinct separation of the protoplasm of the central cell from that of the large tube cell. This separation was the result of plasmolysis, probably due to the killing fluid. The boundary of this cell, however, appeared to be only a plasmic membrane. At least it was exceedingly thin and closely applied to the surface of the protoplasm.

Fig. 3 (Pl. 1) shows the typical arrangement of cells, with two prothallial cells, but between the main part of the pollen grain and the wings there are two spaces cut off by cellulose walls, containing no trace of protoplasm. The writer was unable to decide whether these should be considered as cells or not. They seemed to bear no definite relation to the main part of the pollen grain. In this grain the membrane surrounding the central cell, and continued around the stalk cell, plainly projected beyond the limits of the protoplasm where it had been pulled away from the wall of the pollen grain by plasmolysis. This membrane was very much thinner than the inner cellulose layer of the wall of the pollen grain, but if it was only a plasmic membrane it was at least much firmer than the protoplasm which it bounded, and from which it was partly separated by plasmolysis.

There is shown in Fig. 7 (Pl. 1) a variation somewhat different from those already discussed. Only one disintegrating prothallial cell is apparent, but projecting into the tube cell of the pollen grain is a row of three cells of approximately equal size and structure except that the innermost one of the row is dome-shaped while the others are flattened against the adjacent cells. These three cells have equally large, prominent, and well preserved

nuclei, and apparently either the stalk cell or the central cell of the typical pollen grain has in this case divided again. There was no indication as to which of the two furnished the third cell found here. Another interpretation of this pollen grain is possible. The outermost of the three almost equal cells might be regarded as the second prothallial cell. The writer does not accept this interpretation of that cell because of its large size, its prominent and well preserved nucleus, and its close connection with and general resemblance to the adjacent cell.

A very different type of variation is illustrated in Fig. 8 (Pl. 1). Here the pollen grain, while having the typical form externally, is divided into two equal portions by a wall perpendicular to the long axis of the grain. This wall was very plain where it joined the outer wall of the grain, but where the protoplasm lay against it on both sides it could not be recognized certainly, and it was represented in the drawing only where it was unmistakable. Its position is probably indicated by the cleft in the protoplasm which throws five cells on one side and three on the other. This gives the typical form and arrangement of cells with two prothallial cells on one side, while on the other side of the dividing wall no prothallial cells are formed, and the three cells present apparently represent a stalk cell, a central cell, and a tube cell. The writer believes this difference in the two halves to be of some importance in relation to the variation in number of prothallial cells. If the number of those that disintegrate is invariably two for each pollen grain, which ordinarily has one antheridium, in this double grain where there are two antheridia, there ought to be two disintegrating cells for each antheridium. If it be supposed that one set of two prothallial cells serves as the basis of two antheridia, variation from this arrangement and number of prothallial cells is found in other grains of this same type, containing two antheridia. Fig. 9 shows a grain with the two antheridia in different positions in their respective portions, and each has only one disintegrating prothallial cell visible. Thirty-two grains of this double type were studied in more or less detail. In most of them the two antheridia were placed as in Fig. 8. There was much variation in the number of the prothallial cells connected to the various antheridia. Put in the simplest form and using the single antheridium

instead of the double pollen grain as the basis of comparison the following table shows the amount of variation.

	2 Pr. Cells	1 Pr. Cells	No Pr. Cells	Cells Uncertain	Total Antheridia	Total No. Pollen Grains
No. of antheridia	4	24	18	18	64	32

In the group marked uncertain, the uncertainty was sometimes due to inability to recognize clearly the total number of cells present, and in other cases the position of the wall dividing the pollen grain was uncertain where it ran between the disintegrating prothallial cells. Only one sixteenth of this lot of antheridia shows what has been called the normal number of prothallial cells. Of even more importance than this fact is the further one that in no case did both the antheridia in the same double grain have two prothallial cells, as should have been the case if two is the normal number. There were several cases in which the numbers for the two antheridia were respectively 2 and 1, 2 and 0, 1 and 1, 1 and 0, 0 and 0. In those cases in which there were two prothallial cells in one part, and one or none in the other part of the double grain, it cannot be argued that some had disappeared by disintegration, because the two parts of a double grain are usually at about the same stage of development, and there is no reason to suppose that two cells should so completely disappear in one part, and none in the other. At least some cases should have been found in which both parts of the double grain had two prothallial cells, and most of the double grains should have shown the same number of prothallial cells on the two sides of the dividing wall. Since neither of these conditions was found to exist in the grains examined, and in the light of other facts reported in earlier paragraphs of this article, the writer feels justified in drawing the following conclusions: —

1. The number of disintegrating prothallial cells in the pollen grain of *Picea excelsa* L. is not invariably two, and when a grain is found which shows only one such cell it is not necessarily the *second* prothallial cell and should not be so named. At the most it can only be said that it is uncertain whether the case is one in which a prothallial cell has completely disappeared, or whether it is a case of *normal variation*.

2. The number of vegetative prothallial cells certainly varies from one to three, though the latter number is rare. It may also happen that there are none at all. This condition is comparable with that found in those gymnosperms which typically produce no prothallial cell, as *Juniperus*, *Taxus*, and others. In *Picea* it was found in 3.8 % of the pollen grains that contained only one antheridium.

3. The prothallial cells may vary in position as well as in number. The usual arrangement is dorsiventral, forming a single continuous row with the stalk and central cells, but two prothallial cells may be placed laterally in relation to each other instead of dorsiventrally, and in case of three cells the arrangement may be partly lateral and partly dorsiventral (Pl. 1, Figs. 5, 6).

4. In very rare cases the variation in number may extend to that part of the row of cells which usually is composed of the stalk cell and the central cell. An extra cell may be formed at this point perhaps by division from the central cell. The stalk is then two cells high.

5. The number of prothallial cells formed in the majority of pollen grains would seem to be *one*, if the results obtained in counting are to be fully relied upon, since 66.5 % of them showed but one prothallial cell as against 15.7 % which showed two. This difference is probably greater than it should be, since it cannot be denied that one cell *may* have disappeared in some of those grains which showed only one.

6. The membranes of the prothallial cells sometimes persist after the complete disappearance of the protoplasm, hence they cannot be plasmic, but are probably cellulose. In other cases there is no trace of cellulose walls.

Coker (:04a) interpreted his double pollen grains of *Larix* shown in his Figures 6 and 7, as having been formed by one instead of two divisions of the pollen mother-cell, and the daughter cells having been retained within the mother-cell wall. In the pollen grains of *Picea* studied by the writer this interpretation seems very improbable, first, because no trace of the mother-cell wall was observed around the pollen grain; second, because of the fact that the "wings" of the pollen grain were always present, and always typical in number and arrangement. If these double grains were

contained in a pollen mother-cell, the pollen mother-cell wall was cuticularized and expanded into two wings. No indications of this condition were observed.

A pollen grain with a very different appearance from that of any yet described is represented in Fig. 10 (Pl. 1), which is a drawing of the pollen grain whose discovery led to the observations recorded in this article. In this grain we have the typical tube cell, central cell, stalk cell, and what seem to be two disintegrating prothallial cells, but in addition we find lying along the dorsal wall of the pollen grain a row of four rather prominent cells, each with a nucleus. These cells appear to be of unequal size and of somewhat different shapes. They are separated from the rest of the pollen grain by a wall which was continuous with the inner layer of the wall of the grain, and which appeared just like it in structure. The presence of this wall was made evident by the contracted state of the protoplasm adjacent to it.

The structure of this grain was reported at the meeting of botanists mentioned above, and it was suggested that possibly the four cells represented a prothallium or gametophyte of a much larger size than usual, and the pollen grain showed a reversion to an earlier type of structure. At that time the writer saw no way of determining definitely whether that was the correct interpretation of the structure discovered. In succeeding years, it was found that the class material from which that pollen grain came also contained numerous others similar to it as well as the variations of the different kinds that are reported in this article.

After studying a number of grains of this same type the thought occurred that perhaps a clue to the meaning of the unusual structure might be obtained if the same grains could be studied from the dorsal as well as from the lateral view. Since the pollen grains were mounted in clove oil, this could be done, by causing them to roll over while observing them under the microscope. By repeated trials it was found possible to study some of these abnormal grains from all possible points of view, dorsal, ventral, lateral, and end views. The dorsal and lateral views were the most important.

A total of 22 grains of this structure was studied, and many of them were drawn in two or more views for purposes of comparison. Figs. 11 and 12 (Pl. 1) are respectively the lateral and dorsal

views of the same pollen grain, and Figs. 13 and 14 (Pl. 1) are the corresponding views of another grain. A study of the structure shown in Figs. 12 and 14 as well as others more or less similar to them finally suggested what the writer believes is the correct interpretation of the extra cells along the dorsal wall of pollen grains as shown in Figs. 10, 11, and 13. In Fig. 12 it will be noticed at once that the cells labeled *a* and *b* are like the stalk and central cell in a typical pollen grain, while cell *c* has the same relation to the others as a tube cell, and cell *d* has no corresponding part in the typical pollen grain. No cells appear to correspond to the prothallial cells in the typical grain. In Fig. 14 the correspondence to the typical pollen grain is less clear than in Fig. 12. Nevertheless there is a distinct suggestion of a similar structure. In short, a study of the dorsal view of as many of these grains as possible led to the conclusion that grains of this type are not so very different from the type shown in Fig. 8. They are double pollen grains, but the division wall, instead of running from dorsal to ventral side and dividing the grain into two equal parts, divides it into two very *unequal* parts, and *cuts off the smaller portion along the dorsal wall*. This interpretation was made more certain on looking over all the rough drawings made during the study, when it was found that there was a very complete series of transitional stages between the structure shown in Fig. 8 and that in Fig. 12. In these transitional stages the division wall ran from some point on the dorsal side obliquely toward one of the wings. Fig. 9 is an example of one of these transitional stages, and Fig. 15 is a diagram of what was seen in a dorsal view of a pollen grain with an oblique division wall. The dotted line *xy* is presumably the line of junction of the oblique division wall with the dorsal wall of the grain. This was of course not plain, owing to the oblique position of the receding wall. Cell *a* bulges into cells *b* and *c* like the cell which divides to form the stalk and central cell. Cells *b* and *c* taken together represent the tube cell. If, as is generally supposed, the tube cell represents an antheridium wall, then we have here a case where the antheridium wall is two-celled, a very unusual thing among the gymnosperms. One other case was observed almost exactly like this one, except for a slightly different position of the wall separating cells *b* and *c*. It is just possible that the two tube

nuclei found by Juranyi ('72) in the young pollen tube of *Ceratozamia longifolia* and by Arnoldi (:00) in *Cephalotaxus fortunei* represent two cells in the antheridium wall or tube cell of the pollen grain, but that interpretation can hardly be insisted upon very strongly on the evidence now available.

In the case of the two or more tube nuclei in the pollen tube of angiosperms, the above interpretation ought to be considered, but here there will be even more hesitation over its acceptance than in the gymnosperms.

As regards the large number of nuclei found in the pollen tube of *Agathis* and *Araucaria*, Lopriori concludes that in *Araucaria bidwellii* they are male nuclei, and that the cell-complex which is formed in the pollen tube, and from which they are derived, is a spermatogenous cell-complex. Lopriori's conclusion is evidently much influenced by Juel's discovery of the numerous male cells in *Cupressus*. The present writer cannot accept Lopriori's conclusion until there is direct evidence that the nuclei in question do actually function in fertilization. The reasons for rejecting the conclusion at the present time are these: —

1. The cell-complex from which the nuclei are derived is formed in the pollen grain and not in the pollen tube as Juel found in *Cupressus goweniana*.

2. It is formed, not from a single generative cell, but primarily by the successive unequal divisions of the large cell of the pollen grain, though secondarily the small cells, thus formed may themselves divide in different directions.

These reasons seem sufficient to show that the cell-complex is not spermatogenous in its nature, but that it is the vegetative part of a male gametophyte, and as such is exactly the condition which the present writer thought he had found when he first saw the pollen grain of *Picea* represented in Fig. 10 (Pl. 1). Though this interpretation proved to be wrong for *Picea*, Thompson and Lopriori have probably discovered in the *Araucarineæ* a group of gymnosperms which have the multicellular male gametophyte, and in this particular at least they show the most primitive condition of any of the gymnosperms.

It is to be hoped that these investigators will follow out the full life history of all the cells and nuclei found in the pollen grain and tube of the *Araucarineæ*.

In a recent short review of Lopriori's paper, C. J. Chamberlain also rejects that writer's conclusion that the numerous nuclei are male nuclei, but he gives no reasons therefor except "judging by his figures."

The structure in Fig. 16 (Pl. 1) requires little discussion. It represents one of the somewhat irregular variations in a double grain, but the portion marked *a* seems to consist of a mass of protoplasm completely cut off from the rest, and contains no trace of a nucleus. In order to determine the frequency with which the variation of the double pollen grain occurred, a count was undertaken. Fresh drops of clove oil containing the pollen grains were mounted and all the grains on the slide were systematically counted. A separate list was made of all the grains that were double, both those like Fig. 10 and like Fig. 8 and also the ones intermediate between these two. The total number counted was 1120. Of these there were 27, or 2.4 % which showed the double character more or less plainly. This was a much higher percentage than was expected, but there is no reason to think a mistake was made in the counting. Indeed it is more probable that some of the double grains may have been overlooked. If any of them lay in the position with the dorsal or ventral side toward the observer they would almost certainly have been overlooked since in that position their double nature is very difficult to recognize. The proportion among those that were counted did not impress the observer as being any greater than the proportion among the hundreds that were not counted but were looked over in making the study of the variations found.

As a result of the study of the type of variation shown in Figs. 10-14, the following additional conclusions may be drawn:—

1. The three or four cells lying along the dorsal side of the pollen grain of this type do not constitute a prothallium or gametophyte of unusual size, an interpretation which the writer at one time thought a possibility.
2. They constitute the smaller portion of a pollen grain separated by a division wall into two very unequal portions, each of which may form a more or less typical antheridium.
3. The cells of the larger part of such a pollen grain are similar to the cells in a typical single pollen grain, and cases were observed in which the number of prothallial cells visible was 2, 1, and 0.

4. In the smaller portion of such a double pollen grain there is more variation in the size, number, and arrangement of cells, but generally there is a distinct resemblance to the typical antheridium. In several cases the similarity was striking and unmistakable.

5. In two cases where a cell which is like the one that divides into the stalk and central cell, was plainly marked, the rest of that portion of the pollen grain, which corresponds to the tube cell or antheridium wall, was divided into two cells by an anticlinal wall, that is, the antheridium wall was two celled (Pl. 1, Fig. 15).

6. In the material examined the proportion of double pollen grains was found to be 2.4 % in a count of 1120.

Writers who feel justified in labeling a single prothallial cell as the *second* one, may be inclined to reject some of the conclusions reached in this article, especially the conclusion that a majority of pollen grains in *Picea excelsa* form only one prothallial cell (p. 271) on the ground that so much of the material studied was abnormal. It has already been admitted that there is room for argument as to the *number* of pollen grains in which only one prothallial cell is formed, and the point at issue is really the determination of what is the normal number, or to state it more clearly perhaps, the problem is to determine the limits of variation in the number of cells in the pollen grains of *Picea*, and the relative frequency of the different numbers. Stated in that form, it is apparent that the abnormal, which is only the less frequent, is as much a part of the problem as the normal. The abnormal is only normal variation. Hence conclusions cannot be rejected because based on observation of abnormal structures.

After consideration of both the historical and original parts of this article it is obvious that variation in the number and arrangement of the cells found in the pollen grain and pollen tube is widespread among the families, genera, and species of gymnosperms. They occur in those species which usually have no disintegrating prothallial cells, as well as in those which have one or more such cells. These variations cannot be dismissed with the statement that they are abnormal, since the abnormal is only the less frequent modification. It seems to the writer that they may have a significance beyond the mere fact that the individual species vary.

A comparison between angiosperms and gymnosperms as regards the structure of the pollen grain recalls the well known difference. The essential structure of the pollen is much more uniform among the angiosperms, showing a spermatogenous cell usually free within the larger tube-forming cell, the whole structure to be regarded as probably a gametophyte reduced to an antheridium, the tube cell forming the antheridium wall, and generally there are no prothallial cells. Among the gymnosperms the structure of the pollen grain is not uniform in the different families and genera, and it is not so much reduced as in the angiosperms. In the more complex of the gymnosperms (*Picea* for example) there is not only an antheridium represented, but there may be from one to three disintegrating prothallial cells, and in addition the antheridium has a cell, the so called stalk cell, which has nothing to correspond to it in the angiosperms. This stalk cell is a sister cell to the so called body cell or central cell, which divides to form (usually) two sperm cells, and therefore corresponds to the spermatogenous cell in the angiosperms. In those gymnosperms with the simpler pollen grains no disintegrating prothallial cells are formed, but the stalk and central cells are uniformly present, the mother cell of these two being cut off at one side of the large tube-forming cell. In the pollen of the simplest gymnosperms therefore there is one cell more than in that of the angiosperms, that is the stalk cell. *Cryptomeria* seems nearer to the angiosperms in this particular than any other gymnosperm, since Lawson (:04) has found that the cell cut off at the side of the pollen grain is soon set free and lies within the cytoplasm of the large tube-forming cell. Chamberlain ('97) has also found cases in pollen grains of angiosperms which show one prothallial cell and more often it is found in angiosperm pollen that the spermatogenous cell is cut off at one side of the grain instead of lying free in the tube cell (Coulter and Chamberlain, :03, pp. 134-135).

The gymnosperms then, compose a group containing various transitional stages, as regards the pollen grain structure, between the very reduced condition characteristic of the angiosperms and the condition found among the pteridophytes in which the male gametophyte is more or less developed. Indeed some pteridophytes as *Isoetes* and *Selaginella* have more reduced male gametophytes than some gymnosperms, as *Picea* and *Pinus*.

The facts just presented suggest the question whether the gymnosperms at the present time are in a process of retrogressive modification in the direction of the condition found in the pollen of the angiosperms, or have the gymnosperms reached a condition of stable equilibrium, not so much reduced as that of the angiosperms and with different groups of genera stable at different stages in the reduction process.

The mental attitude of those investigators who insist on labeling a single prothallial cell as the second one implies a stable condition, with the number of cells formed invariable, and this mental attitude seems to be the common one among the writers on the subject. It seems to the present writer, however, that the number and wide distribution of the variations found among the gymnosperms may indicate that the gymnosperms, or at least some of them, are not in a state of stable equilibrium as regards the structure of the pollen grain, but that the process of reduction of the male gametophyte is in progress. In *Picea*, for example, a very few cases were found in which three vegetative prothallial cells were seen, 15.7 % of the grains counted showed two, 66.5 % showed one, and 3.8 % showed none. The number in others was uncertain. In the case of the double pollen grains divided into nearly equal parts, several showed no prothallial cell in one part, and a few showed none in either part. The extreme limits of variation in the number of prothallial cells in the pollen grain of *Picea excelsa* are therefore from 0 to 3, with 1 as the number of greatest frequency.

These facts do not *prove* that *Picea* is in a condition of progressive reduction of the male gametophyte, but at the very least they allow that interpretation, and it is set forth merely tentatively. Other investigations may either confirm or disprove it. Should further investigations confirm this conclusion we should have a case of a structure changed by gradual modification rather than by mutation. The occasional variations found in angiosperms in which the pollen grain shows a vegetative prothallial cell, or several tube nuclei, or the spermatogenous cell cut off at one side of the grain instead of lying free in the cytoplasm of the tube-cell (Coulter and Chamberlain, :03, p. 134-135) may possibly have a similar significance. If so, the condition now found in the pollen

of angiosperms also has come about by gradual modification, and the variations mentioned show that the "normal" structure is not so firmly fixed but that a small proportion of the grains produced reverts to a condition which was a stage in the gradual development. If this interpretation of the variations is rejected, then they must be looked upon as mutations, for whose cause we have nothing at all to suggest.

It is worth noting that among the gymnosperms the reduction of one structure in the pollen grain is not necessarily accompanied by the reduction of other structures in the same pollen grains. For example in *Cupressus* (Coker, :04) no sterile prothallial cell is cut off, and yet many sperm cells are formed instead of only two (Juel, :04). On the other hand, *Picea*, which may have as many as three sterile prothallial cells not only has the sperms reduced to two nuclei in one cell but even one of those nuclei has undergone a further reduction in size and only one, the larger, is functional (Miyake, :03). In the reduction of the sperm cells therefore, some of the gymnosperms have been modified to even a greater extent than the angiosperms. The degree of reduction seems to be closely associated with "use and disuse" of the parts concerned. Reduction of one of the sperm cells takes place only in cases where both could not function in fertilizing the egg. In the angiosperms the second sperm cell functions by uniting with the polar nuclei to form the endosperm, and this functioning whether a true fertilization or not, has been sufficient to prevent the reduction and possible suppression of one of the sperm cells.

The observations of Miyake (:03) that in *Abies balsamea* the second sperm nucleus may divide, or attempt to divide before it disintegrates in the upper part of the egg, and especially the observation that in one case this second sperm nucleus united with one of the second segmentation nuclei of the fertilized egg, is suggestive as to the possible way in which "double fertilization" may have arisen. The sperm nucleus that is left over after the union of the other one with the egg nucleus, has a tendency to unite with any nucleus that may be available, and in the angiosperms the polar nuclei offer the opportunity for such a union. It is not at all necessary that either of the polar nuclei be the homologue of an egg as Bonnier (:05) believes, in order to explain the union

with the male nucleus, since the latter has been shown to be able to unite with a purely vegetative nucleus, even of the sporophytic generation. This observation of Miyake's seems therefore to strengthen the evidence that the endosperm of angiosperms was vegetative phylogenetically (Coulter and Chamberlain, :03, p. 183), and to weaken correspondingly the view that it was strictly sexual in its origin (Bonnier, :05) and that the endosperm is to be regarded as a modified embryo.

If the introduction of the characters of the male parent into the endosperm modified that endosperm so as to make it produce food more suitable to the embryo with characters inherited from the same male parent (Sargent, :00, p. 708) then the embryo would be more vigorous, and more fit to survive in the struggle for existence than the one not nourished by such an endosperm. Hence those individual plants in which "double fertilization" took place would finally become dominant in the competition with others of the same species.

The reduction, disintegration, and final complete suppression of the vegetative part of the male gametophyte may also depend on the law of "use and disuse." The vegetative cells of a well developed male gametophyte function chiefly in the process of photosynthesis. In most of the gymnosperms this function is impossible since the pollen grain is soon enclosed in the micropyle and light is excluded by the thick scales of the fertile cone. It is then a waste of energy and food materials to form cells that do not function, and this waste is only in part compensated for, if the cells formed disintegrate later and thus become available as food for the work necessary in forming sperms. Disuse leads to disintegration of the useless cells, and their complete suppression is the most advantageous condition of all.

It is interesting to note in this connection that in *Araucaria* which probably has the well developed male gametophyte, the pollen grain does not enter the micropyle (Thompson, :05), but germinates at the distal end of the ligule, more or less entangled on its serrated edge. From this point the pollen tubes pass in the grooves on the surface of the ligule or scale, a distance of an inch or more, to the micropyle. It would seem from this description of Thompson's that the pollen grains are exposed to the light during the development of the tubes, hence the multicellular male

gametophyte present may function in photosynthesis. Continued use has prevented in this case the reduction which took place in those species in which the pollen grain enters the micropyle directly.

In addition to the specific conclusions in regard to *Picea* (see pp. 270 and 275) the following more general ones are drawn, some of which are suggested rather than demonstrated:—

1. The variations in the male gametophyte and other structures in the pollen of gymnosperms, indicate that in this group there are examples of progressive reduction of some of those structures.

2. This reduction is by a gradual modification and not by mutation, and is due to the disuse of the vanishing structures.

3. The different structures are not necessarily reduced to a corresponding degree in the same species.

4. The suppression of the male gametophyte in gymnosperms is a distinct advantage where the function of photosynthesis is impossible to it.

5. The occasional prothallial cell in the pollen of angiosperms indicates that in this group also there was a reduction by gradual modification.

6. The division of the non-functional male nucleus in the egg of some of the gymnosperms and its fusion with a segmentation nucleus of the fertilized egg in *Abies balsamea*, strengthens the evidence for the view that the endosperm of angiosperms is phylogenetically a modified gametophyte and not a modified embryo.

7. The extremes in the variation of the male gametophyte among the genera of gymnosperms are found in *Araucaria* with a gametophyte of from 20 to 44 cells, (provided my interpretation of Lopriori's observation is correct) and *Cryptomeria japonica* (Lawson, :04), in which there is not only no vegetative male prothallium, but in which even the division wall between the tube nucleus and the primary spermatogenous nucleus is so fugitive as almost to escape detection.

The writer has no intention of making any further investigations along this line, as his special interests lie in another direction, but he felt that the opportunity to make the observations here recorded, though arising only incidentally, ought not to be neglected.

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ANATOMY OF *CRYPTOBRANCHUS ALLEGHENIENSIS*

ALBERT M. REESE

THE SKELETON

The Skull

SINCE the skull of *Cryptobranchus allegheniensis* is strong and largely composed of bone, it is easy to prepare and to study. Figs. 1 and 2, A and B, are dorsal and ventral views of the skull proper and of the lower jaw, taken from photographs.

The skull as a whole has essentially the same structure as that of the Japanese giant salamander, described and figured by Osawa (:02), but it differs from the latter somewhat in general outline and in the shape of some of its constituent bones. Its length is greater in proportion to its width than is the case with the Japanese species, and the anterior outline of the head, formed by the maxillary and premaxillary bones, is more rounded in the American species, in which it forms an almost perfect arc of a circle. In the Japanese form the maxillæ and premaxillæ, as figured by Osawa, are relatively heavier than in the American species, and the posterior ends of the maxillary bones approach more closely the anterior borders of the pterygoids. The shape of the lower jaw is about the same in both species, but, if anything, is narrower in the American salamander, so that it does not fit with very great precision against the upper jaw. The anterior border of the skull is formed, as has been said, by the maxillary and premaxillary bones (Figs. 1, 2, 3, *Mx.*, *P. Mx.*), both of which are armed with numerous small, conical teeth, there being about 12 on each premaxilla, and 38 on each maxilla, making 100 teeth in the entire row.

The cartilaginous portions of the skull are not so extensive as in the Japanese salamander, and are superficially visible in the region of the anterior nares only, the anterior part of the orbit, the auditory region, and the articular surface of the quadrate.

FIG. 2.—A. Dorsal view of mandible. B. Ventral view of skull (from a photograph). A., angular; C., minute canals through parasphenoid; C. C., carotid canal; Co., coronoid; D., dentary; Mx., maxillary; O., occipital; Or., orbit; Pa., parasphenoid; P. Mx., premaxillary; Po., preotic; Pt., pterygoid; Q., quadrate; S., squamosal; V., vomer.

The bony cranium will first be described, and then a brief description of the cartilaginous cranium will be given.

The *premaxillæ*, forming the extreme anterior tip of the skull, are firmly united with each other in the middle line, and articulate less closely, on each side, with the adjacent *maxillæ*. Their dorsal surface is prolonged backward somewhat, to articulate with the anterior borders of the nasals. Between them, in the mid-dorsal line, is a small foramen, and each of them exhibits a small foramen on its anterior surface (Fig. 1, *P. Mx.*). Their antero-ventral border is armed with the teeth above mentioned, while the postero-ventral border articulates with the anterior border of the vomers (Fig. 2, *P. Mx., V.*). About half of the median border of the nasal opening (*N.*) is formed by the premaxilla.

The two *maxillary* bones (*Mx.*) form the rest of the upper jaws, and make up, in fact, about three fourths of their extent. Their entire ventral border is armed, as has been described, with a single row of teeth. The medial end of their arc is in articulation with the premaxillary, while the lateral end tapers somewhat and is connected with the anterior angle of the pterygoid by a tough band of connective tissue. On the dorsal aspect of the maxillary, near the medial end, a triangular projection extends in a postero-medial direction between the frontal and the prefrontal. On the anterior border of each maxilla, at the base of the triangular projection just described, are two small openings, the infra-orbital foramina.

The *nasals* (Figs. 1 and 3, *Na.*) lie just back of the premaxillæ and form the posterior half of the median border of the anterior nares (*N.*). The two bones, when taken together, have somewhat the shape of an arrowhead, the tip of the head pointing towards the base of the skull. The base of the arrowhead articulates anteriorly with the posterior projections of the premaxillæ that have already been mentioned. In the mid-dorsal line the two nasals articulate closely with each other, while their postero-lateral borders articulate with the frontal bones. The anterior half of each nasal is closely united, ventrally, with the dorsal side of the corresponding vomer, and thus helps to form the septum between the two nasal chambers.

The *frontals* (*F.*) are two large, much elongated bones that lie

just posterior to the nasals and form a considerable part of the roof of the skull. Like the nasals, these two bones, when taken together, have somewhat the shape of an arrowhead, the tip of the head again being towards the posterior. Along the middle line, where the bones articulate with each other, is sometimes seen a well marked ridge. Each frontal forms the posterior half of the lateral border of the corresponding nasal opening, and articulates laterally with the maxillary, prefrontal, and parietal; anteriorly with the nasal, and medially with its fellow of the opposite side. Ventrally the frontals are more or less closely united with part of the cartilaginous cranium, to be described later.

The *prefrontals* (*Pf.*) are two elongated bones in the roof of the skull, on the antero-medial border of the orbits. Each bone articulates anteriorly with the corresponding maxilla, medially with the frontal, and posteriorly with the extreme anterior end of the parietal.

The *parietals* (*P.*) are two large bones that form the greater part of the roof of the cranial cavity. The posterior half of each bone is broad and angular, while the anterior half is long and narrow, and extends forward to articulate with the posterior end of the prefrontal, as has already been stated. The posterior halves of the two parietals articulate with each other, but the narrow anterior portions are separated from each other, and into the space thus formed the posterior ends of the two frontals project and articulate. The narrow, anterior part of the parietal overlies and is more or less closely attached to the ethmoid, presently to be described. The broad, posterior part of the parietal articulates laterally with the squamosal, and posteriorly with the lateral occipital. The sagittal suture, between the two parietal bones, extends back to the antero-dorsal border of the foramen magnum. A very small portion of this border is formed by the medio-posterior extremities of the parietals.

The *ethmoids* (*E.*) will be described at this place, although they are partially composed of cartilage even in the adult, and are described by Osawa in connection with the cartilaginous cranium. The ossified portion of the ethmoid is shown at *E.* in Figs. 1 and 3. It is an elongated rod of bone, attached dorsally to the parietal, as has been mentioned, and ventrally to the parasphenoid

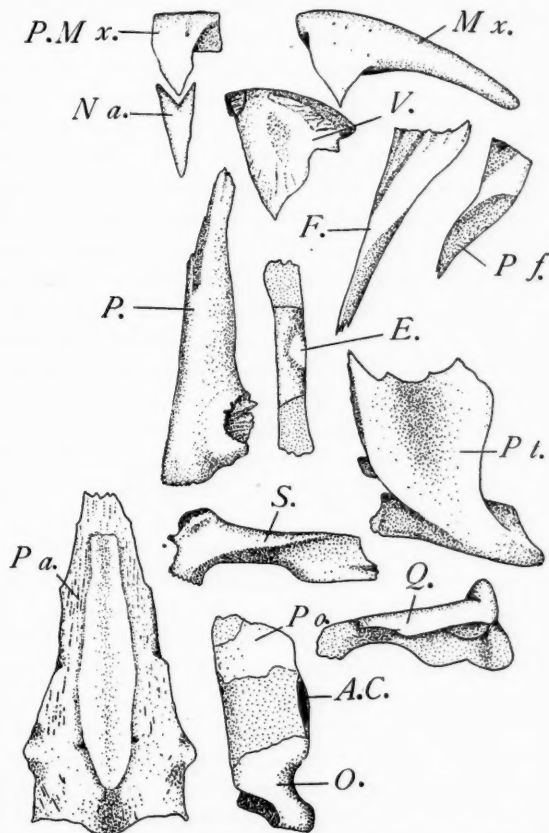


FIG. 3.—The bones of the skull, disarticulated. A. C., opening of the auditory capsule; E., ethmoid (cartilaginous at each end); F., frontal; Mx., maxillary; Na., nasal; O., occipital; P., parietal; Pa., parasphenoid; Pf., prefrontal; P. Mx., premaxillary; Po., proötic; Pt., pterygoid; Q., quadrate; S., squamosal; V., vomer.

and, slightly, to the pterygoid. Extending laterally through the midventral region of this osseous part of the ethmoid is a small ethmoidal canal (E. C.). Anteriorly and posteriorly the osseous ethmoid is continuous with the cartilaginous cranium of the nasal and the occipital regions.

The *pterygoid* (Pt.) has, with the exception of the parasphenoid,

a greater surface than any bone in the skull. Seen from the dorsal aspect, it is nearly rectangular in outline, but seen from the ventral side, it exhibits a long, postero-laterally projecting process which underlies the squamosal and quadrate bones. Its anterior and lateral borders are thin, and the former makes the irregular outline of the posterior border of the orbit. The antero-lateral corner is connected with the maxillary by a band of connective tissue, as has already been pointed out. The median border underlies the ethmoid to a slight extent, and is attached ventrally to the side of the parasphenoid. The posterior border is hidden, in a dorsal view, by the squamosal and quadrate, with which it articulates. The above-mentioned postero-laterally projecting process of the pterygoid is an elongation of the lateral and posterior borders, and extends entirely across the squamosal until it shows behind it, and forms a part of the articular surface for the lower jaw. This projection of the pterygoid behind the squamosal and quadrate is shown in Fig. 1. The pterygoid is somewhat arched from side to side, with the convexity of the arch dorsad. Above the postero-median corner of the pterygoid, in the angle between the ethmoid, the parietal, and the squamous, is a marked depression (see Fig. 1) covered in life by a membrane. In the bottom of this depression several canals leading into the cranial cavity may be seen. One of these canals is much larger than the others, and is said by Osawa to be for the exit of the trigeminal nerve. At the postero-lateral corner of the depression is a short canal, formed by a narrow space left between the squamosal above and the pterygoid below. This canal does not lead into the cavity of the skull, but extends backward to the outer side of the auditory capsule, and seems to be an anterior continuation of the vertebral canal; it is apparently the canal that Osawa calls the palatine.

The *squamous* bones (*S.*) are among the most important in determining the shape of the skull. They are elongated, rod-shaped bones that extend laterally, at right angles to the long axis of the skull, and form the square outline of its base. Each bone has the appearance of being slightly twisted, due to a well marked dorsal ridge that extends nearly its entire length. The medial end of the bone is somewhat flattened and enlarged, and articulates with the side of the parietal near its posterior end.

The distal end of the squamosal is firmly united with the enlarged end of the quadrate, and partially overlies that bone. Ventrally the squamous articulates with the posterior border of the pterygoid as has been described.

The *quadrate bones* (*Q.*) are two small bones that form almost the entire articular surfaces for the lower jaw. A small portion of these surfaces, however, is formed by the pterygoids. Each quadrate is a small, triangular bone lying at the distal end of the squamous above described, and largely covered by it. The heavy, basal portion of the bone projects beyond the end of the squamous and, together with the tip of the pterygoid, is covered with a thick pad of cartilage for articulation with the lower jaw. The slender, medially projecting portion of the bone lies anterior and ventral to the squamous, and dorsal to the pterygoid. It is more closely attached to the former than to the latter bone. Osawa figures the quadrate in the adult skull as entirely of cartilage, and describes it with the cartilaginous cranium, but in the present form it is quite fully ossified.

The *tympanic bones*, described by Osawa in the Japanese species, could not be determined.

The *exoccipitals* (*O.*) form the greater part of the border of the occipital foramen. Each bone presents a postero-laterally projecting condyle, for articulation with the first vertebra. Through the base of this condyle passes a horizontal canal of considerable size into the posterior part of the cranial cavity. This canal is probably for the exit of the vagus nerve. The anterior part of the exoccipital is much enlarged and is hollowed out to form the posterior half of the auditory capsule. The dorso-anterior borders of the exoccipital articulate with the posterior end of the parietal, while the ventral border articulates with the posterior end of the parasphenoid.

The *occipital foramen* or foramen magnum is markedly triangular in outline, especially when seen from the dorsal aspect. The apex of the triangle, which lies at the posterior end of the sagittal suture, is some distance in front of the base, so that the plane of the aperture, instead of being vertical, slants in a dorso-anterior direction. Only a small portion of the base or ventral border of the foramen is formed by the parasphenoid.

All of the bones described above are seen in a dorsal view of the skull; those of the bony cranium that will now be described, are best seen from the ventral aspect.

The *parasphenoid* (*Pa.*) is the only unpaired bone in the skull, and is larger than any other single bone. It forms practically the entire floor of the cranial cavity, as seen from the exterior. The bone as a whole has somewhat the shape of a broad, blunt-pointed dagger, with the point towards the anterior end of the skull, and partially concealed, in a ventral view, by the posterior ends of the vomers, with which it articulates (*Pa.* in Figs. 2 and 3). Laterally the parasphenoid articulates, for the anterior half of its length, with the pterygoids. Just posterior to the pterygoids it articulates dorsally with the small proötics, and posterior to the auditory foramen it articulates with the exoccipitals. Its extreme posterior end forms the ventral border of the occipital foramen. A short distance anterior to this point is seen, in some specimens, a well defined, irregular transverse line (Fig. 2), which would seem to indicate the presence of a basioccipital bone, but as no separation of the bone along this line could be effected, the presence of a definite basioccipital could not be determined. On each side of the parasphenoid, close to its point of union with the proötic, is a canal (*C. C.*), leading into the cranial cavity, called by Osawa the carotid canal. Nearer the midventral line, somewhat anterior to the preceding, are two very small openings (*C.*), probably for the entrance of minute blood vessels. The ventral surface of the parasphenoid is smooth and nearly flat, except at the anterior end where it is more or less convex, with a slight median ridge that fits in between the posterior ends of the vomers.

The *vomers* (*V.*) are the large flat bones that form the base of the anterior end of the skull and the floor of the nasal cavity. They may, perhaps, be considered as formed of the fused vomers and palatines. Each bone is roughly triangular in outline, one side of the triangle being fused with the corresponding side of the other bone in the midventral line. Another side, which is rather deeply indented by a sort of bay, forms part of the inner border of the orbital space; and the third side, which is in the form of an arc and is armed with teeth, is attached to the maxilla and premaxilla. The row of teeth, lying on anterior borders of the two vomers,

forms an arc that is almost exactly concentric with the arc of the premaxillæ and maxillæ, except that there is a slight depression in the middle where the two vomers meet. The anterior half of the median edge of each vomer is elevated dorsally into a ridge, and the median elevation formed by the union of these ridges separates the nasal chamber into its two parts, and unites the vomers below with the nasals and the premaxillæ above. It forms, in other words, the bony nasal septum.

The *proötics* (*Po.*) are two small bones of irregular shape that form the antero-dorsal borders of the auditory capsules. Even in the adult they are largely composed of cartilage, so that in the dried skull they scarcely show from either the dorsal or the ventral side. They are more closely united to the parasphenoid than to any other bone, but they also articulate with the cartilaginous posterior end of the ethmoid, with the parietals, with the squamous bones, and, possibly to a slight extent with the pterygoids. There are several canals that lead from the exterior to the cranial cavity, in the neighborhood of the proötic. Of these the largest has already been mentioned in connection with the pterygoid bone, and is said by Osawa to be the trigeminal foramen. It is a break in the median border of the proötic, rather than an actual canal through the bone. The only other canal in this bone that can be made out without difficulty is the facial, which lies in the edge of the bony part of the proötic, just dorsal to the carotid canal, and runs transversely through the bone to the cranial cavity.

Columella auris is the name given to two very small bones that are found in connection with the auditory capsules. Each columella is fan-shaped or palmate in outline, and, on account of its minute size and loose attachment to the rest of the skull, is easily lost in the preparation of the skull. The broad part of the bone is connected by cartilage with the foramen ovale of the auditory capsule, while the narrow end (the handle of the fan) projects laterally and, according to Osawa, is connected by cartilage with the quadrate, though this latter point could not be determined in the present species. The columella does not show in either of the figures of the skull.

The cartilaginous cranium will now be described. It may be divided, to use the terms adopted by Osawa, into two general

regions, an anterior naso-ethmoidal and a posterior petroso-occipital, regions which are connected by two narrow longitudinal bands in the position of the ethmoids. The space between these bands is the pituitary space, and the bands themselves are ossified in their middle regions to form what we have already described as the ethmoid bones, while their ends are cartilaginous to connect anteriorly and posteriorly with the naso-ethmoid and petroso-occipital regions respectively.

The *naso-ethmoid cartilage* serves chiefly as a lining to the nasal chamber, and may be seen in a dorsal view of the skull, over a part of the anterior nares and at the antero-lateral angle of the orbital space.

The *petroso-occipital* region is more extensive, and the cartilage is there thicker than in the naso-ethmoidal region. It forms, as the name would suggest, the cartilaginous basis of the occipital region, and though in the adult it is largely ossified, there is a considerable cartilage that persists even in the adult skull. The thickest cartilage is found in the region of the ear, where it forms a large part of the auditory capsule. Various parts of the petroso-occipital region are more or less fully ossified to form the following bones, whose form and position have already been described, and which are described by Osawa in connection with the cartilaginous cranium: the exoccipital (*occipitale laterale*), the proötic, the quadrate, and the columella. The ethmoid, which forms the middle of the longitudinal bands connecting the petroso-occipital and naso-ethmoidal regions, has also been described in connection with the bony cranium.

It remains now to describe the bones and the cartilages of the visceral skeleton.

The Visceral Skeleton

The *visceral skeleton* is made up of six arches: the mandibular arch or lower jaw, the hyoid arch, and four visceral arches. It differs, then, markedly from the Japanese species which, according to Osawa, has only four arches, the last two visceral arches being absent. The visceral skeleton as a whole is large and strong and, though consisting largely of cartilage, it persists throughout

life. It forms the supporting framework to the floor of the capacious mouth and throat so important in the process of inspiration.

The *mandible* or lower jaw (Figs. 1, 2, 4) is made up of two distinct parts, joined together anteriorly, in the middle line, by a short ligament of cartilage, the mandibular symphysis. As may be seen from the figures, the curve of the anterior margin of the mandible is not so wide as that of the upper jaw, so that the two jaws do not fit together very closely. Each half of the mandible is made up of three elements: the dentary, the coronoid, and the angular.

The *dentary* (*D.*) is the largest of these three bones, and extends from the symphysis almost to the posterior angle of the jaw. Its anterior end is thick and rounded, while the posterior end is thin and pointed to fit against the outer surface of the angular. The ventro-anterior surface of the dentary is smooth, and is marked by a series of about six small openings, mental foramina, which do not show in either a ventral or a dorsal view of the mandible. The dorso-posterior, or upper-and-inner, border of the dentary is depressed to form a deep alveolar surface, along the outer border of which are situated the small, conical teeth in a single row. There are about forty-five teeth in each dentary. The alveolar surface extends for somewhat more than two thirds of the entire length of the bone, and ends posteriorly at the point where the dentary meets the outer border of the coronoid. The teeth are all of nearly the same size, except that those at the posterior end of the row are slightly smaller than the rest. They are attached to the bottom and side of the alveolar depression, so that their crowns sometimes project but a short distance above the upper border of the dentary bone.

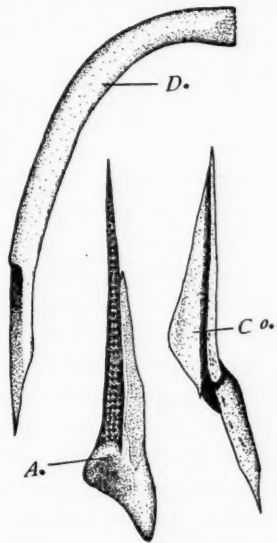


FIG. 4.—The bones of the mandible, disarticulated. A., angular; Co., coronoid; D., dentary.

Individual teeth are frequently broken off, but whether they are ever regenerated again the writer is not able to say.

The *coronoid* (*Co.*) is a spindle-shaped bone that lies on the inner side of the mandible near its posterior end. Its inner or medial surface is smooth and rounded except near the middle of its length, where it is elevated and roughened to form the coronoid process for the attachment of muscles. In the anterior corner of the triangular depression between the dorsal borders of the dentary and coronoid bones is a small canal leading towards the anterior end of the jaw. It may be called the alveolar canal. A ventral view of the jaw shows a more evident canal (*Ct.*) entering between the dentary and coronoid bones, just at the anterior end of the angular, as seen from the surface but really at some distance behind this end as the anterior portion of the angular is hidden between the two other bones. This canal corresponds, perhaps, to the inferior dental foramen of higher forms. The canal that Osawa describes, in this region, passes directly through the coronoid bone; he calls it the "canalis chordæ tympani." The outer surface of the coronoid (hidden, of course, by the other bones) is deeply grooved longitudinally to receive a long, slender process of the angular (Fig. 4).

The *angular* (*A.*) forms the posterior end of the mandible and presents there an articular surface for attachment to the quadrate. This articular surface is triangular in outline, with the apex of the triangle towards the posterior. The articular portion of the angular is a thick mass of cartilage, and extends forward to fill the angular space between the dentary and coronoid bones that has already been mentioned. Anterior to this angular space, this cartilage is continued forward as a long, slender rod (Meckel's cartilage) lying in a furrow between the dentary and the coronoid. Meckel's cartilage extends for nearly three fourths of the length of the jaw, or to about the middle of the row of teeth. The part of the angular that is seen from the ventral aspect (Fig. 1, A) is ossified, and extends, as may be seen from the figure, for some distance, anteriorly, between the dentary and the coronoid. In fact it extends farther in an anterior direction than is seen from the surface, being covered for some distance by the coronoid.

The *hyoid apparatus* (Fig. 5), using that term to include both

the hyoid and the visceral arches, has, as may be seen from the figure, a very complicated structure. It differs from the same apparatus in the Japanese salamander in having two more visceral arches, as has been said; also in the relative amounts of bone and cartilage, and in the general form of the constituent parts. The arches will now be described in order, from before backward.

The *hyoid arch* (*H.*, *H'*., *C.*) is, as would be expected, much the largest of the arches, and is composed of two S-shaped bars united medially by a small, unpaired copula (*C.*). Each bar is made up of two closely united segments (*H.*, *H'*.), of which the anterior one (*H'*.) is nearly straight and is united with the copula, while the posterior one (*H.*) is strongly curved outwards at its free or posterior end where it ends

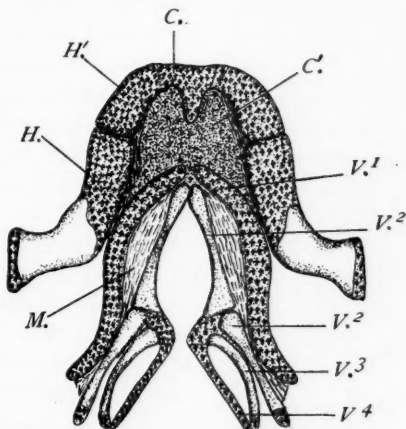


FIG. 5.—The hyoid apparatus. *C.*, copula of hyoid arch; *C'*., copula of first and second visceral arches; *H.*, *H'*., elements of the hyoid arch; *M.*, membrane between the first and second visceral arches; *V*¹⁻⁴., first to fourth visceral arches.

in a cartilaginous surface for articulation with the skull. As may be seen in the figure, nearly half of the posterior segment of the hyoid arch is bony (the cartilaginous portions being, in all cases, dotted). In the Japanese form the entire hyoid arch is composed of cartilage, and each bar is of a single piece, instead of being of two pieces as in the present form. The copula or median connecting piece is of about the same shape in both species, and consists of a short transverse portion with a pointed knob projecting in a postero-dorsal direction. The elements of the hyoid arch are flattened in a dorso-ventral direction, so that they are elliptical in cross section. The whole hyoid arch has somewhat the shape of a wide letter U, with the free ends of the letter bent widely apart. Into the space between the two bars of the hyoid arch projects the

flat, cartilaginous copula (C') of the first and second visceral arches. It is flat, broadly heart-shaped in outline, and is composed of soft, fibro-cartilage. It is united around its periphery with the inner border of the hyoid arch by a thin but tough connective-tissue membrane. On the midventral line of this copula, at its posterior edge, in a slight cartilaginous elevation to which are attached the anterior ends of the first and second visceral arches, the former to its lateral, the latter to its posterior border.

The *first visceral arch* (V^1) is composed of two slender, somewhat flattened, S-shaped bars united in the median line by the copula that has already been described. Each bar of this arch is composed of a single rod of firm, translucent cartilage. Along its entire median border this arch is united, by a tough, fibrous membrane, to the outer border of the *second visceral arch* (V^2) which, in distinction to the preceding arches, is composed almost entirely of bone. Its constituent bars, instead of being S-shaped, are practically straight laterally though somewhat arched in a dorso-ventral direction. Viewed from the ventral aspect, the two bars of this arch form an almost perfect letter V. Each bar is formed of two elongated bones, of which the anterior or dorsal one is the longer. Both bones are nearly circular in cross section, and are enlarged at each end, the two adjacent ends being the larger, and somewhat flattened. The free end of the posterior or ventral bone is tipped by a small piece of cartilage.

Between the two bones of the second visceral arch, on each side, is a small pad of cartilage which extends medially and becomes spread out for the attachment of the anterior ends of the *third* (V^3) and *fourth* (V^4) *visceral arches*, of which the former is composed almost entirely of bone, and the latter entirely of cartilage. The third and fourth arches are formed of distinct bars; that is, they are not united in the midventral line by a copula as are the preceding arches. The bars of the third and fourth arches on each side are united with each other at both ends, and form a loop which serves to stiffen the border of the permanent gill slit. The third bar is of bone, and is tipped at the posterior end with a small head of cartilage for attachment to the corresponding end of the fourth bar. This bar is cylindrical in cross section, and is slightly curved, so that the loop is kept permanently open, while

the elasticity of the cartilaginous fourth bar allows considerable variation in the size of the loop and consequently in the size of the gill slit. The anterior end of the third bar is united, for a short distance, with the posterior bone of the second bar by the same tough membrane that was noted in connection with the more anterior arches.

The Vertebral Column

The vertebral column of the American salamander (Fig. 6) consists of from 39 to 42 bones or vertebræ. The giant salamander of Japan, according to Osawa, has in its vertebral column forty-five vertebræ, besides two cartilaginous rudiments at the tip of the tail. The vertebræ may be divided into three sets: those of the body, of which there are 19; those of the tail, 19 to 22 in number; and a single vertebra between these two sets, the sacrum. The number of body vertebræ, as might perhaps be expected, seems to be more constant than the number of caudals, though the variation in the latter may be partly due to the great difficulty of preserving the last few vertebræ on account of their small size and cartilaginous nature. All of the vertebral centra, with the exception, of course, of the anterior surface of the first, are deeply amphicelous. The anterior and posterior concavities are so deep that they almost meet in the middle of the centra. There is, however, no continuous passage through the centra.

As a type of the body vertebræ, or those lying anterior to the sacrum, the tenth vertebra may be described (Figs. 6 and 7). As is seen in Fig. 7, D, a lateral view, the centrum is distinctly hourglass-shaped, and its length is about twice its greatest diameter. Like all of the other body vertebræ, except the first, this vertebra



FIG. 6.—Dorsal view of the entire vertebral column, with the ribs attached (from a photograph).

has strongly developed transverse processes (Figs. 6, 7, 8, *T.*), to which are attached short, thick ribs (*R.*). These ribs, like the processes to which they are attached, are flattened in an antero-posterior direction, so that, at their points of attachment, they are considerably thicker in a dorso-ventral direction than they are in an antero-posterior direction. The ribs, with the exception of those attached to the sacrum (to be presently described), stand out at right angles from the vertebræ, and taper to a sharp, round point. In the anterior part of the body the ribs are somewhat longer than the processes to which they are attached, while in the region near the sacrum they are shorter. The transverse processes are of about the same length on all of the body vertebræ, and project rather strongly towards the posterior. The base of

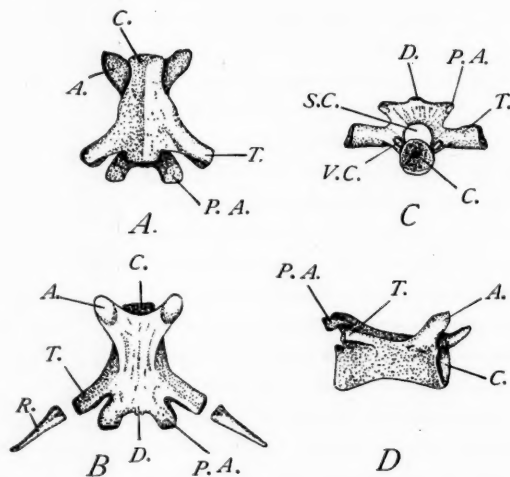


FIG. 7.—Four views of the tenth vertebra. A, Ventral. B, dorsal. C, posterior. D, lateral. A., anterior articular process; C., centrum; D., dorsal spine; P. A., posterior articular process; R., rib; S. C., spinal canal; T., transverse process; V. C., vertebral canal.

each transverse process is perforated by a small vertebral canal (Fig. 7, *V. C.*). The dorsal or spinous process (Figs. 7 and 8, *D.*) is small and inconspicuous in all of the body vertebræ, and is most prominent on the first.

The posterior articular processes (Fig. 7, *P. A.*) have a rounded outline, as seen from above, and are flattened ventrally where they articulate with the underlying anterior processes of the succeeding vertebra. The anterior articular processes (Fig. 7, *A.*) do not differ greatly from the posterior, except in having their articular surfaces on the dorsal instead of the ventral side. The vertebrae of the body region resemble each other so strongly in shape that it would be very difficult to say from just what part of the body any given vertebra had been taken, but in an individual skeleton the vertebrae in the middle region of the body are both longer and heavier than those anterior and posterior to them.

The sacral vertebra differs from those immediately in front and behind it only in the much greater development of the transverse processes (Fig. 6, *S.*), and the ribs. The sacral ribs, since they serve for the attachment of the pelvic girdle, are much heavier and stronger than any of the other ribs. Instead of projecting as sharp points straight out from the body, they curve downward and end in articular surfaces for the attachment of the upper ends of the two rods of the ilium.

The caudal vertebrae present more variations both in size and form than do those of the body. The first caudal vertebra so closely resembles the last body vertebra that it would be very difficult, if not impossible, to tell them apart. The third caudal vertebra may be described as a type of those of this region (Figs. 6 and 8). The chief differences between this vertebra and the typical body vertebra are, besides the smaller size of the former, the weaker transverse processes, the larger dorsal spine, and the presence of a well developed hæmal arch. Transverse processes are found on the first eight of these vertebrae, and are provided, at least in the case of the first four or five, with minute ribs. These processes diminish in size from before backward, so that those of the eighth caudal vertebra are very small (Fig. 6). The dorsal spines, on the other hand, become more prominent from before backward, until they reach their greatest development in the mid-caudal region, or, at any rate their greatest relative development. As the caudal vertebrae become more and more compressed laterally, the posterior articular processes approach each other until, in the midcaudal region, they are not distinguishable from the

large dorsal process. Even in the third caudal, these processes (Figs. 6 and 8, *D.*, *P. A.*) have the appearance of being mere articular surfaces on the sides of the spinous process. The anterior articular processes (Figs. 6 and 8, *A.*) also diminish in size towards the posterior until, on the last few vertebræ, they, like the posterior articular processes, practically disappear, and the vertebræ in this region are united by their centra only.

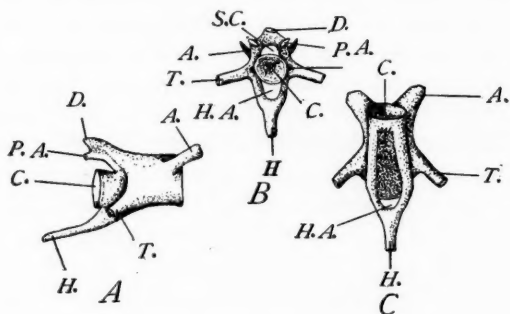


FIG. 8.—Three views of the third caudal vertebra. A, lateral. B, posterior. C, ventral. A., anterior articular process; C., centrum; D., dorsal spine; H., hælmal spine; H. A., hælmal arch; P. A., posterior articular process; S. C., spinal canal; T., transverse process.

The hælmal arch, which is characteristic of the caudal vertebræ, is well developed on the third vertebra (Fig. 8, *H. A.*), in which the two sides of the arch are prolonged ventrally into a long spine (*H.*). As may be seen in Fig. 8 the canal formed by the hælmal arch is larger than the spinal canal; this is true of all the caudals except the first, which is without a hælmal arch.

The hinder caudal vertebræ, besides being laterally compressed, show an actual concavity in each side of their centra.

The two cartilaginous rudiments at the end of the tail, that are described by Osawa, I have not been able to determine, though I am not willing to say that they do not exist in the American as well as in the Japanese form. There is, however, except in the number of vertebræ, a strong resemblance between the vertebral columns of the two animals.

Skeleton of the Appendages

The Anterior Extremity.—Both pairs of appendages are small and weak, and the two girdles are largely made of cartilage. The shoulder girdle is almost entirely composed of cartilage, and the scapular, which is small, is the only part that is bony.

The *sternum* (Fig. 9) is so small and is composed of such thin cartilage that it may easily be overlooked in a hasty dissection. It lies in the usual midventral position, and is overlapped anteriorly for about half of its length by the large coracoids, that is to say, the coracoids overlap it on its ventral side. In a medium-sized specimen it is about 2.5 centimeters long and of nearly the same width. It is somewhat shovel-shaped, with the rounded edge towards the anterior (Fig. 9). The ventral aspect is smooth and slightly convex, while the dorsal side is correspondingly concave, and is provided with a V-shaped thickening, which projects slightly in an antero-dorsal direction. It is chiefly by this thickening that the sternum is attached to the body wall. The edges of the sternum thin out so gradually that it is difficult to determine where the cartilage ends and the fibrous tissue begins.

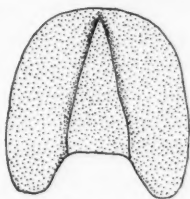


FIG. 9.—Dorsal view of the sternum.

The *coracoids*, which are described by Osawa as being composed of two parts, the procoracoids (Fig. 10, *P. C.*) and the coracoids (*C.*) proper, though there is nothing to distinguish the two regions, are by far the most conspicuous elements of the shoulder girdle. They are composed entirely of cartilage and, together with the sternum, form a complete, though thin cartilaginous sheath for the ventral side of the thoracic region of the body. They overlap each other almost completely, as each sheet extends almost to the opposite side of the body. Like the sternum the coracoid is very thin, especially at the edges, but, unlike the sternum, it has no thickening on either side for muscular or connective tissue attachments. At the outer edge the coracoid becomes considerably thickened, where it articulates with the scapular and with the humerus. With the scapula it is firmly united, but with the humerus it forms a ball-and-socket joint, the glenoid cavity (Fig.

10, *Gl.*) being rather deep to receive the rounded head (*H'*) of the humerus (*H.*). The center of the coracoid is perforated by an irregular aperture of varying size (*F.*), called by Osawa the "supracoracoid foramen."

The *scapula* and *suprascapula* (Fig. 10, *Sc.*, *S. Sc.*) form, together, a spatula-shaped structure whose area is small in comparison with that of the coracoid, with which it is firmly united. The suprascapula forms the blade of the spatula, and is a broad, thin sheet of cartilage, somewhat curved to conform to the curvature of the side and back of the animal's body. The scapula is

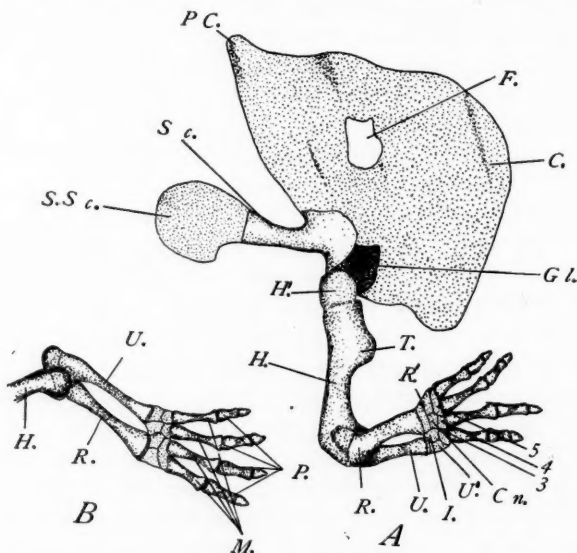


FIG. 10.—Anterior appendage. A, entire appendage. B, distal portion in a different position. C., coracoid; Cn., centrale; F., foramen; Gl., glenoid cavity; H., humerus; H', head of humerus; I., intermedium; M., metacarpals; P., phalanges; P.C., procoracoid; R., radius; R', radiale; Sc., scapula; S. Sc., suprascapula; T., tuberosity of humerus; U., ulna; U', ulnare; 3, 4, 5, distal row of carpals.

an elongated, somewhat flattened structure, slightly enlarged at one end, where it is attached to the suprascapula, and considerably enlarged at the other, where it is attached to the coracoid. It is the only part of the shoulder girdle that is composed of bone.

The *humerus* (Fig. 10, *H.*) is rather thick in proportion to its

length, and articulates with the glenoid cavity of the coracoid by the round, cartilaginous head (H'). Its more or less cylindrical shaft is marked by a large tuberosity ($T.$) near its proximal end, and is separated from the head by a well marked neck. At its distal end it is broad, somewhat as in the human humerus, and articulates with both the radius and the ulna.

The *radius* and the *ulna* are entirely distinct from each other, and take nearly equal parts in the formation of both elbow and wrist joints, though the ulna, as is usual, is the more closely associated with the humerus. The ulna (Fig. 10, $U.$) is slightly longer than the radius ($R.$), and strongly resembles the corresponding bone in the human arm, though it is, of course, not so long in proportion to its diameter, and its shaft is not so nearly cylindrical in section. Its proximal end is enlarged to form the concave articular surface, the sigmoid cavity, and its distal end is also slightly enlarged, and is provided with a disc of cartilage of considerable thickness. The radius presents no peculiarities in structure. It enlarges rather rapidly from the center towards each end, where well marked discs of cartilage are found.

The *carpus*, though composed entirely of cartilage, shows with considerable distinctness the seven elements of which it is made up. Two elements articulate with each of the forearm bones: on the radial side are the radiale (R') and the centrale ($Cn.$), the latter lying in about the center of the carpus; on the ulnar side are the ulnare (U') and the intermedium ($I.$). Uniting the four elements above described with the metacarpals are three distal carpals (Fig. 10, 3, 4, 5), one of which is united with two of the metacarpals. On the anterior appendage are four digits, each of which is made up of an elongated metacarpal element ($M.$) and two short phalangeal elements ($P.$), of which the more distal tapers to an almost claw-like sharpness. The two middle digits which are of about the same length, are somewhat longer than the two outer ones. There is no sign, on the fourth digit, of the third phalangeal element described by Osawa in the Japanese salamander. The relative sizes of the metacarpal and phalangeal elements are about the same in each of the four digits.

The Posterior Extremity.—The posterior extremity, consisting of the pelvic girdle and the hind legs, is a rather curious mixture

of cartilage and bone. Its structure, in general, agrees closely with the corresponding region in the Japanese species, as described by Osawa, except in regard to the epipubis, which is markedly different.

The *pelvic girdle* will first be described. Taken as a whole, it has a roughly triangular form. The apex is formed by the anteriorly directed epipubis, while the basal angles are formed by the dorso-posteriorly directed ilia. Its ventral surface is somewhat convex, and, along its posterior half, is marked by a slight, median, longitudinal ridge for the attachment of muscles. Its dorsal surface is concave, with the most marked concavity between the bases of the two ilia (Fig. 11). The greater part of the pelvis is made up of the pubis, which is divided into two parts, the pubis proper, and the epipubis.

The *pubis* proper is a shield-shaped plate of cartilage (Fig. 11, *P.*), whose ventral convexity and dorsal concavity have been mentioned in speaking of the pelvis as a whole. It is almost completely divided into lateral halves by a median suture which is especially evident at the posterior end of the pelvis, between the two ischia (Fig. 11, *S.*). On each side of this suture, slightly anterior to the middle region, there is a small opening (Fig. 11, *O. F.*), the obturator foramen. The posterior corners of the pubis are elevated for the attachment of the ilia (*I.*), and under these elevations the deep, well developed acetabula are situated.

Anteriorly, the pubis is prolonged into a long, cartilaginous *epipubis* (*Ep.*), which, instead of being forked as in the Japanese salamander and some other Amphibia, is a straight rod, slightly broadened and flattened at its distal end and somewhat enlarged both laterally and dorso-ventrally at its attached end. The union of the pubis and epipubis is a close one, but allows considerable freedom of motion.

Firmly united with the posterior end of the pubis, and continuous with it, are two oblong plates of bone, the *ischia* (*Is.*). Together, the ischia form a blunt, posteriorly projecting process to the pelvis. The ischia are separated along the middle line by the median suture, but their adjacent edges are not quite parallel, so that a slight cartilage-filled space is left between them at one place. There is also a small triangular piece of cartilage at their extreme posterior end.

The *ilia* (*I.*), like the ischia, are of bony consistency, except at their extremities, where there is a small amount of cartilage. They are somewhat curved in a postero-dorsal direction, and are considerably enlarged at their pelvic end, and less so at their sacral end.

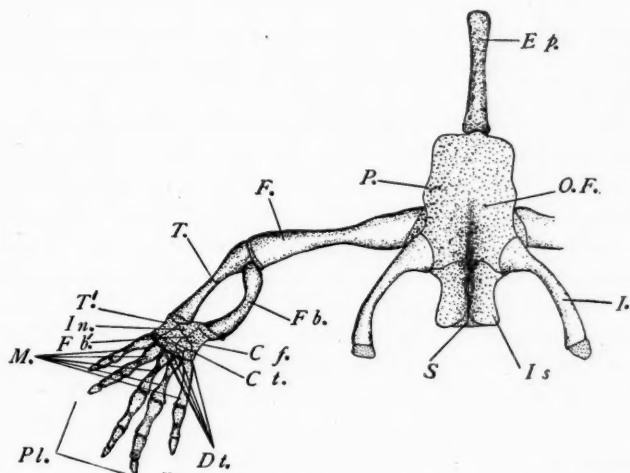


FIG. 11.—Posterior appendage, from the dorsal aspect. *Cf.*, centrale fibulare; *Ct.*, centrale tibialis; *Dt.*, distal row of tarsal elements; *Ep.*, epipubis; *F.*, femur; *Fb.*, fibula; *Fb'.*, fibulare; *I.*, ilium; *In.*, intermedium; *Is.*, ischium; *M.*, metatarsus; *Of.*, obturator foramen; *P.*, pubis; *Pl.*, phalanges; *S.*, suture; *T.*, tibia; *T'*, tibiale.

The *femur* (Fig. 11, *F.*) is rather more slender in proportion to its length than it is in the Japanese animal. Its proximal end is enlarged to form a round, cartilaginous head, which articulates with the deep acetabular cavity that has already been mentioned. On the ventral side, near the proximal end, is a sort of trochanter, or roughened projection for the attachment of muscles. The shaft tapers rapidly from the enlarged proximal end to about the middle length of the bone, where it is nearly cylindrical in cross section, and is not more than half the diameter of the head. The distal half of the femur is much broadened, in a dorso-ventral direction, and flattened in an antero-posterior direction. This marked flattening does not show in the figure because of the posi-

tion in which the leg is drawn. This distal enlargement of the femur is slightly convex on its anterior surface, and concave on its posterior surface. On the convex anterior surface is a very slight ridge, which is prolonged distally as an inconspicuous knob. Almost the entire distal end of the femur articulates with the tibia, but there is a small articular surface for the proximal end of the fibula. Between the distal end of the femur and the proximal ends of the tibia and fibula is a layer of cartilage of considerable thickness.

The lower leg is made up of two entirely distinct bones, the tibia and fibula. Of these bones, the tibia (Fig. 11, *T.*) is larger and will be described first. It is considerably larger at its proximal than at its distal end, and forms almost the entire articular surface of the knee-joint. The proximal end is broadened and flattened in the same planes as is the distal end of the femur, with which it articulates. On the anterior surface of this end is a slight ridge, corresponding to the ridge that has been noted on the distal end of the femur. The shaft of the tibia tapers rapidly from the proximal end to a point a little beyond the middle of the bone, and then increases in size to form the somewhat flattened distal enlargement, which articulates with the tibiale and centrale of the foot. The flattening of the distal end is in the same plane as that of the more enlarged proximal end. The distal, like the proximal end, is provided with a well developed plate of cartilage.

The *fibula* (Fig. 11, *Fb.*) is not so long as the tibia, and, as is shown slightly exaggerated in the figure, is strongly bowed on the tibial side. The side away from the tibia is only slightly bent, so that the bow is chiefly due to the shape of the surface next to the tibia. The enlargement at the proximal end is rounded, and articulates laterally with the side of the tibia and proximally with the distal end of the femur. The shaft of the bone is somewhat flattened, so that it is elliptical instead of circular in cross section. The distal end is more enlarged than the proximal, but is flattened instead of being rounded. At the extreme end of each flattened surface is an inconspicuous depression, not shown in the figure. The fibula, like most of the other bones that have been described, ends, both proximally and distally, in cartilage.

The *tarsus*, like that of the Japanese species, is composed of

ten cartilaginous elements, which are arranged in two more or less definite groups, the proximal and the distal, with two elements in an intermediate position. Articulating with the tibia, or rather with the cartilage that tips the distal end of the tibia, is the *tibiale*, (*T'*) an irregular, elongated mass of cartilage. Attached in the same way to the fibula is the *fibulare* (*Fb.'*); and lying in an intermediate position and articulating more or less with tibia, fibula, tibiale, and fibulare is the angular *intermedium* (*In.*). The distal row of tarsal elements (*Dt.*) is composed of five masses of cartilage, all of about the same size, and each attached to the basal end of one of the metatarsal bones. These distal cartilages are smaller than the proximal. Between the proximal and the distal rows, are two small elements (sometimes fused into one) called by Osawa the "*centrale tibiale*" and "*centrale fibulare*" (*Ct.* and *Cf.*).

The *metatarsus* (*M.*) is composed of five elongated, cylindrical bones, somewhat enlarged as usual at the ends. They are of nearly the same length, though the first (on the tibial side) is somewhat shorter than the rest, and the third and fourth are somewhat longer.

The *phalanges* (*Pl.*) of the first, second, and fifth digits are made up of two elements, while those of the third and fourth digits contain three elements each. The terminal element of each digit is a pointed, claw-like structure.

THE VASCULAR SYSTEM

For the purpose of working out the course of the blood vessels the usual method of injecting the arterial and venous systems with masses of different colors was used. The injection of the arterial system was accomplished with but little difficulty by inserting the cannula into the well developed conus arteriosus, and through it forcing the injection mass into all of the arteries. But the injection of the veins was a more difficult matter, and will be described in connection with the description of those vessels.

The Arterial System

From the anterior edge of the ventricle leads forward the thick-walled conus arteriosus (Fig. 12, *T.*). It is of considerable length, and is more or less bent towards the right. It becomes considerably enlarged anteriorly to form the conspicuous bulbus arteriosus (*B.*). The bulbus arteriosus gives off from its anterior end, on each side, four branchial vessels (Fig. 12, 1, 2, 3, 4), which diverge slightly as they pass towards the side. All four of these arches are united with one another, just beyond the gill cleft (*G. C.*), but it is from the second and third that the real systemic arch (*S.*), is chiefly formed. This complicated arrangement of the branchial blood vessels is, in the main, similar to that described in the Japanese hellbender by Osawa, but differs considerably from the description given by Chapman ('93), also of the Japanese salamander.

The first arch, which may be called the *carotid*, extends for some distance as a single vessel and then becomes slightly swollen to form a sort of *carotid gland* (*C. G.*), similar to that found in the frog. From the median side of the carotid gland is given off an artery which is distributed to the hyoid apparatus and the floor of the mouth, and may hence be called the *lingual* (*L.*).

Just beyond the carotid gland the arch divides and reunites again, giving off one or two small vessels to the neighboring parts. Then, after continuing for some distance as a single vessel, it divides into two vessels, the *external* and *internal carotids* (*E. C.*, *I.*). Just before dividing into the external and internal carotids the arch is connected with the main systemic arch by a vessel that is called by Marshall the ductus Botalli, by Osawa the ramus communicans (*Com.*).

The *second* and *third branchial arches* (Fig. 12, 2, 3), after running more or less parallel to each other to a point back of the carotid gland, unite to form the main *systemic arch* (*S.*). The third arch runs along the anterior margin of the gill cleft (*G. C.*), and gives off, just before uniting with the second arch, a branch to the fourth branchial arch. This branch may be called the ductus Botalli (*D. B.*).

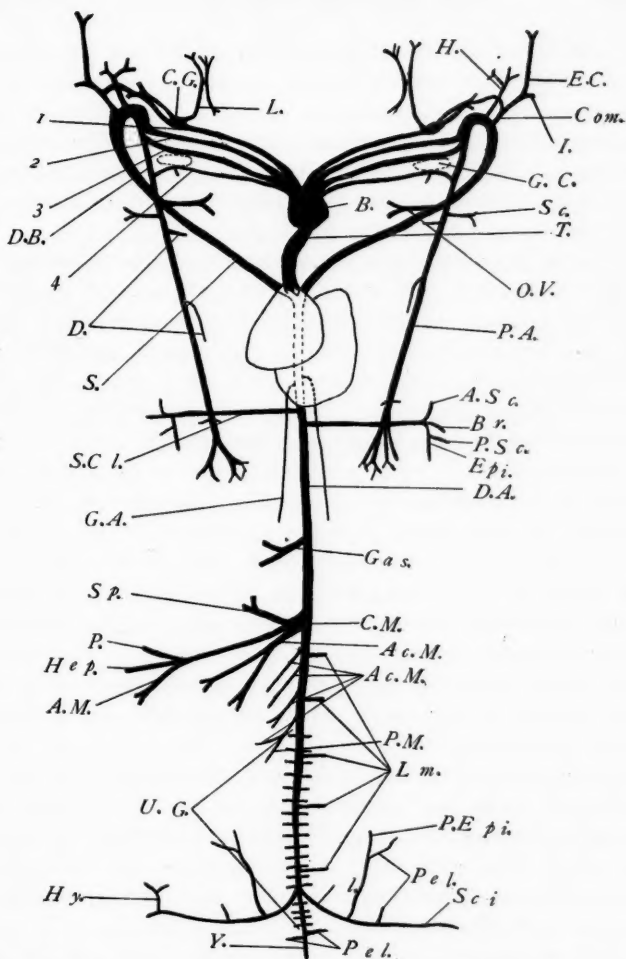


FIG. 12.—The arterial system, ventral aspect. A. M., anterior mesenteric; Ac. M., accessory mesenteric; A. Sc., anterior scapular; B., bulbous arteriosus; Br., brachial; C. G., carotid gland; C. M., coeliaco-mesenteric; Com., ramus communicans; D., to dorsal region, near lungs; D. A., dorsal aorta; D. B., ductus Botalli; E. C., external carotid; Epi., epigastric; G. A., anterior genital; Gas., gastric; G. C., gill cleft; H., hyoid; Hep., hepatic; Hy., hypogastric; I., internal carotid; Il., iliac; L., lingual; Lm., lumbar; O. V., occipitovertebral; P., pancreatic; P. A., pulmonary; Pel., pelvic; P. Epi., posterior epigastric; P. M., posterior mesenteric; P. Sc., posterior scapular; S., systemic arch; Sc., scapular; Sci., sciatic; S. Cl., subclavian; Sp., splenic; T., conus arteriosus; U. G., urogenital; Y., caudal; 1, 2, 3, 4, first to fourth branchial arches.

A short distance beyond the point of union of the second and third arches, the systemic arch gives off a well marked vessel (*H.*), to the end of the hyoid apparatus, and some distance beyond this it gives off an occipito-vertebral artery to the vertebral column and occipital region (*O. V.*). After passing around to the dorsal side of the digestive tract, the two systemic arches unite, just above the heart, to form the dorsal aorta (*D. A.*).

The *fourth branchial arch* passes just posterior to the gill opening, at the outer margin of which it is connected with the third arch by the ductus Botalli. Beyond the ductus Botalli it gives off an artery (*Sc.*) to the region of the scapula, and then two small arteries (*D.*) to the muscles of the dorsal part of the body in the region of the lungs. The main branch of this arch continues posteriorly as the pulmonary artery (*P. A.*).

Some variation in the relative sizes of the vessels of the branchial region occurs as well as some slight variation in their distribution, but the normal condition is about as described above.

The distribution of the blood vessels that arise as branches of the dorsal aorta will now be described. The aorta and its branches are so easily filled with the injection fluid that it is a comparatively easy matter to work out their distribution, especially in the abdominal region. In fact, the only part of the arterial system that offers any difficulty is the outer part of the visceral arches, in the region of the gill openings.

The branches of the aorta will be described in order from before backward. The most anterior branches are given off in the region of the heart, as a pair of rather small arteries (Fig. 12, *G. A.*) which arise nearly opposite each other and extend in a posterior direction to supply the anterior part of the reproductive organs, especially the oviducts.

A short distance posterior to the last described arteries, are given off the two *subclavians* (*S. Cl.*), the right vessel arising a little anterior to the left. As might be expected from the slight development of the anterior appendages, the subclavian arteries are comparatively small vessels. On reaching the shoulder girdle, each subclavian divides into four main branches. The most anterior of these (*A. Sc.*) supplies blood to the region in front of the scapula. The next branch (*Br.*) is the brachial, and extends

into the fore leg. The third branch (*P. Sc.*) extends to the region posterior to the scapula, and also probably, to the posterior border of the fore leg. The most posterior branch of the subclavian (*Epi.*) runs in a posterior direction, and carries blood to the lateral part of the body back of the anterior leg; it is called by Osawa the epigastric.

Some distance posterior to the subclavians is seen an unpaired vessel (*Gas.*) which sends branches to the lesser curvature of the stomach, and may be called the gastric. The next artery, which may be called the cœliaco-mesenteric (*C. M.*), is a rather large one, and branches almost immediately into three parts. The most anterior of these branches (*Sp.*) supplies the greater curvature of the stomach, and also the spleen, and may be called the splenic. The second branch of the cœliaco-mesenteric divides into three smaller branches: a pancreatic (*P.*) supplying the pancreas; a hepatic (*Hep.*) supplying the liver; and a third branch, the anterior mesenteric (*A. M.*), which carries blood to the anterior third of the small intestine.

The most posterior of the three branches of the cœliaco-mesenteric artery is distributed to the small intestine posterior to the region supplied by the anterior mesenteric; it is the first of several vessels that supply blood to the posterior two thirds of the small intestine, and that might be called accessory mesenterics (*Ac. M.*). There are three unpaired accessory mesenterics posterior to the one just described, and a fourth is formed as one of the two divisions of another unpaired branch of the dorsal aorta (*Ac. M.*). There are thus five of the so called accessory mesenteric arteries.

The artery (*P. M.*), with which the most posterior of the accessory mesenterics unites to form a single vessel is the posterior or inferior mesenteric and supplies blood to the anterior third of the large intestine. Five or six rather large, unpaired arteries (*Lm.*) are given off by the aorta, at more or less regular intervals, between the origin of the cœliaco-mesenteric and the iliaes. These lumbar arteries pass into the body wall along the mid-dorsal line.

Numerous pairs of urogenital arteries (*U. G.*) are given off by the aorta in the abdominal region, and supply the kidneys and reproductive organs. On account of the great elongation of the kidneys in a posterior direction, the last of the urogenital arteries

lie as far back as the cloaca or even posterior to it. In the neighborhood of the cloaca, the dorsal aorta gives off a pair of large arteries, the iliacs (*Il.*) which are continued into the posterior appendages as the sciatic arteries (*Sci.*). Each iliac artery gives off, a short distance from its origin, a vessel, the posterior epigastric (*P. Epi.*), which is chiefly distributed to the ventral body wall, but which also sends blood to the pelvic region (*Pel.*). A short distance distal to the posterior epigastric, each iliac gives off a small artery to the pelvic region. From the right iliac an additional artery is given off, distal to those just described, to the bladder and the posterior end of the rectum. This is the hypogastric (*Hy.*).

Posterior to the point of origin of the iliac arteries, the aorta continues backward, with diminished caliber, as the caudal artery (*Y.*) to supply blood to the tail. Besides several pairs of renal arteries, there is given off from the aorta, just back of the iliacs, a pair of arteries (*Pel.*), to supply blood to the dorsal region of the pelvis. This completes the description of the more important vessels of the arterial system. Without stopping to describe the distribution of the more minute vessels, the venous system will now be described.

The Venous System

The venous system is much more difficult to work out than the arterial system, due chiefly to the difficulty of obtaining good injections, especially in the region anterior to the heart.

The venous system, as described in this paper, will exhibit more differences from that described by Dr. Osawa for the Japanese giant salamander than were seen in connection with the arterial system. The veins of the posterior region of the body were injected, without especial difficulty, as follows: the abdominal vein was injected both forwards and backwards; the portal vein was injected forwards, beginning so far towards the tail that practically the entire system was filled; and the posterior vena cava was injected by cutting off the tail and inserting the cannula into the caudal vein. The veins of the anterior parts of the body were injected through the anterior venæ cavæ, and it was here

that the greatest difficulty was experienced in getting the injection fluid into the smaller vessels, in fact, it was only by repeated injections at various points that even the more important veins of this region could be filled. The posterior end of the posterior cardinal veins could not be filled with the injection mass, even after repeated attempts, so that the connections of these veins, if any exist, with the other veins of the abdominal region could not be made out.

The conspicuous, thin-walled *sinus venosus* (Figs. 13 and 14, *S. V.*) into which the blood from the various parts of the body is emptied, is formed mainly by the union of three large veins: the two superior venæ cavæ (*S. C.*), and the inferior vena cava (*I. C.*). The pulmonary veins (*L.*), bringing blood back to the heart from the lungs, as their name would indicate, unite with each other dorsal to the sinus venosus, and empty into the latter at a point whose exact location is difficult to determine on account of the small size of these pulmonary vessels. The superior vena cava of the right side seemed in most, if not all cases, to be attached to the apex of the ventricle. What the object of this attachment might be, was not determined. Each superior vena cava is formed by the union of the following veins: the innominate (*In.*) which is practically nothing more than the lateral continuation of the superior cava itself, the external jugular (*E. J.*), and the posterior cardinal (*Car.*).

The external jugular collects blood chiefly from the lower side of the head, and is formed by the union of two veins which probably correspond to the mandibular and lingual or laryngeal, though they could not be traced to their origin.

The posterior cardinal (*Car.*) empties into the superior cava at a point nearly opposite the opening of the external jugular. Throughout most of its course it lies deeply buried in the muscles of the dorsal body wall, and, as has been said, its extreme posterior termination could not be determined, owing to the impossibility of obtaining a complete injection. It was traced backward as far as the anterior end of the kidney, but whether beyond that point it is simply lost in the body wall or is connected with some of the veins of the abdominal region, could not be determined. Near its anterior termination the posterior cardinal is

joined by a vessel (*S.*) from the region of the shoulder, and a short distance posterior to this point it is connected, by a sort

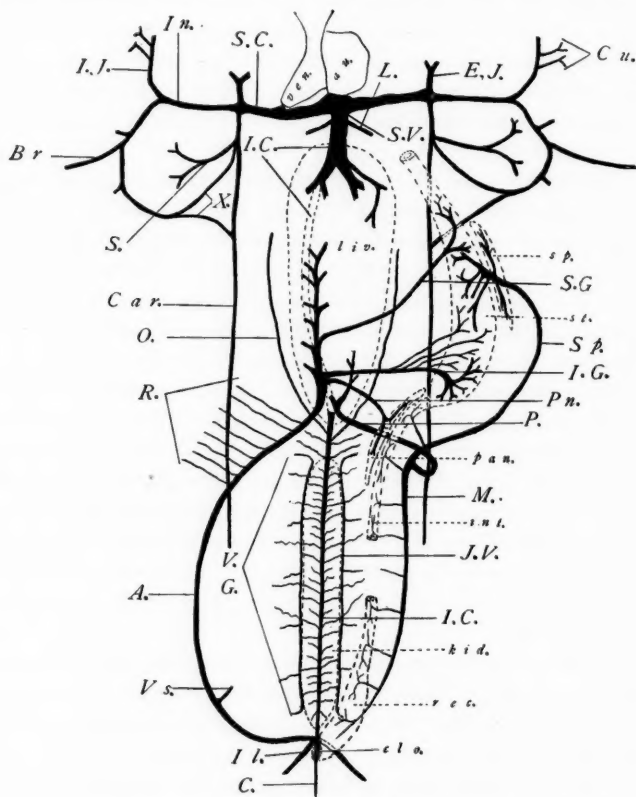


FIG. 13.—The venous system, ventral aspect. *A.*, abdominal; *Br.*, brachial; *C.*, caudal; *Car.*, posterior cardinal; *Cu.*, cutaneous; *E. J.*, external jugular; *G.*, genital; *I. C.*, inferior cava; *I. G.*, inferior gastric; *I. J.*, internal jugular; *Il.*, iliac; *In.*, innominate; *J. V.*, vein of Jacobson; *L.*, pulmonary; *M.*, mesenteric; *O.*, oviduct; *P.*, portal; *Pn.*, pancreatic; *R.*, parietals; *S. C.*, superior vena cava; *S.*, from shoulder; *Sp.*, splenic; *S. V.*, sinus venosus; *V.*, vertebral; *Vs.*, from urinary bladder; *X.*, plexus.

of simple plexus of veins (*X.*), with the brachial vein (*Br.*) which brings blood to the heart from the anterior appendage. To the brachial and to the plexus of veins just mentioned, are added a

number of small veins from the region of the shoulder. The innominate vein (*In.*) is formed by the union of the internal jugular (*I. J.*) and the brachial (*Br.*). The main branch of the former returns blood from the interior of the skull, and is joined shortly before its union with the brachial, by two smaller vessels (*Cu.*), leading from the side of the head. The brachial, as might be expected from the small size of the fore leg, is a comparatively small vein. This completes the description of the vessels connected with the superior venæ cavæ, as the vessels of the two sides of the body in this region are alike.

The veins of the abdominal region will now be described. Since these vessels are usually injected without difficulty, their distribution may be made out with comparative ease. One of the largest and most noticeable veins in the body is the *abdominal* (*A.*). It adheres closely to ventral body wall, slightly to the right of the median line, and, unless care be taken, may easily be cut in opening the abdominal cavity. In the diagram it, like the veins from the stomach and intestines, is for the sake of clearness drawn towards the side. Posteriorly it is formed chiefly by the union of the two iliac veins (*Il.*), a union which takes place just anterior to the cloaca (*clo.*). The iliac veins return the blood from the posterior appendages, and, like the brachial veins, are of comparatively small size. A short distance anterior to the point of union of the iliac veins the abdominal vein receives a very small vein (*Vs.*) from the urinary bladder. Into the most anterior quarter of the abdominal vein, near to its junction with the liver, empty several (eight or nine) veins, the parietals (*R.*), which return blood from the ventral body wall. Anteriorly, the abdominal vein enters the liver, a little in front of the apex, and becomes broken up into capillaries, though it may be traced along the ventral surface of the liver for a considerable distance in an anterior direction.

The arrangement of the veins from the stomach and intestines, the *hepatic-portal system*, is rather peculiar, and will now be described. The blood from practically the entire length of the intestines, both small and large, is collected by a single vein (*M.*) which may be called the mesenteric. A short distance posterior to the liver, this vein unites with the splenic vein (*Sp.*) to form the

main branch of the portal vein (*P.*) through which the blood finds its way into the liver. The splenic vein, as its name would indicate, collects blood from the spleen, but it brings blood also from the middle region of the stomach. The greater part of the blood from the stomach is collected into two well marked veins, the superior and inferior gastrics (*S. G.*, *I. G.*) which empty into that part of the abdominal vein which has already been described as extending for some distance along the ventral side of the liver. Of these two gastric veins, the inferior is the larger, and empties into the abdominal vein at some distance behind the superior gastric. Emptying into the abdominal at almost the same place with the inferior gastric, is a vein of considerable size, the pancreatic (*Pn.*). The portal vein proper, then, brings blood to the liver from the intestines and the spleen; but most of the blood from the stomach and apparently all that from the pancreas is carried into the liver through the abdominal vein.

It now remains only to describe the system of the *inferior vena cava*, and especially that part of the system that lies posterior to the liver. The blood from the tail is collected into a caudal vein (*C.*) that, after entering the abdominal cavity, becomes the inferior or posterior vena cava (*I. C.*). This posterior part of the inferior cava lies between and slightly ventral to the kidneys, and is so closely associated with these organs, from which it receives numerous veins, that its individuality as a distinct vessel seems almost lost. Extending along the distal sides of the kidneys, and connected at frequent intervals by small vessels with the inferior cava, are the more or less distinct veins of Jacobson (*J. V.*). Each vein of Jacobson receives about six vertebral veins (*V.*) from the corresponding side of the vertebral column. On account of the great number of the renal veins and the close attachment to the kidneys of the veins of Jacobson, the details of these veins are difficult to determine.

The blood from the reproductive organs is emptied into the inferior cava through several pairs of genital veins (*G.*), some of which lie anterior to the kidneys while some cross the anterior ends of these organs to reach the inferior cava. In the female, a comparatively large vein leads from the anterior end of each oviduct to empty into the inferior cava just behind the liver (*O.*).

The inferior cava enters the liver near the apex of the right lobe. By carefully dissecting away the substance of the liver, the course of this large vein may be followed entirely through that organ. It extends in a nearly straight line through the dorso-lateral part of the right lobe, and emerges from the anterior surface of the liver as the large thin-walled vessel that empties into the heart. Just before, or at about the time of its emergence from the liver, it is joined by the large hepatic vein, so that that part of the inferior vena cava which is anterior to the liver is many times as large as that part which is posterior to the liver. This completes the description of the more important peripheral vessels of the vascular system; and it now remains to describe the structure of the heart.

The Heart

The heart lies far forward in the body, just anterior to a line joining the front legs. It is protected ventrally by the broad underlying cartilages of the procoracoids and the sternum, to which it lies so close that they must be removed with some care in order not to cut into the pericardial cavity. The size of the heart is moderate in relation to the size of the entire animal, and seems to vary considerably, even in animals of the same approximate size. It has the vitality usually seen in cold-blooded animals, and will continue to beat for a considerable time after being removed from the body, or after being filled with the injection fluid.

External Anatomy.—When seen from the ventral aspect (Fig. 14, A), it presents six main regions: the conus arteriosus, the bulbus arteriosus, the ventricle, the right and left atria or auricles, and the sinus venosus. These regions may be seen from the dorsal aspect as well, if the heart be dissected from the body (Fig. 14, B), and they will now be described in turn. Their form and relative size will vary somewhat, of course, with their state of distension at the time they are sketched. The heart from which the figure was made, was moderately well filled with the injection fluid, and differs considerably in general appearance from Osawa's figures of the heart of the Japanese salamander.

The bulbus arteriosus (*B.*), to begin at the most anterior region of the heart, is a striking object, seen on removing the skin and the

cartilages of the pectoral girdle from the ventral side of the throat. It is of a whitish color, and its walls are tough and thick. Anteriorly it divides to form the arterial arches of each side, and posteriorly it narrows suddenly to form the truncus, which connects with it at somewhat of an angle, instead of entering exactly in the middle line. Its ventral surface is smooth and even, while its dorsal surface may be more or less grooved longitudinally, as seen in the figure. In cross section it is elliptical, and is compressed in a dorso-ventral direction.

The conus arteriosus (*C.*) is a well marked tubular structure

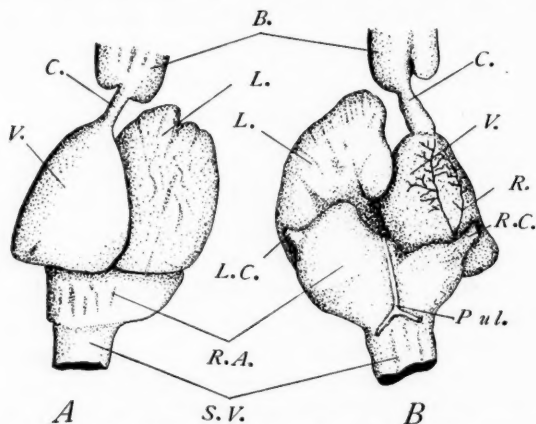


FIG. 14.—The heart. A, ventral. B, dorsal aspect. *B.*, bulbus arteriosus; *C.*, conus arteriosus; *L.*, left auricle; *L. C.*, left anterior vena cava; *Pul.*, pulmonary; *R.*, coronary vessels; *R. C.*, right anterior vena cava; *S. V.*, sinus venosus; *V.*, ventricle.

leading from the anterior angle of the ventricle, and becoming enlarged at its anterior end to form the bulbus arteriosus that has just been described. It is unusually long, and its cylindrical shape and tough walls make it an excellent place into which to insert a cannula for the purpose of injecting the arterial system.

The ventricle (*V.*) is a thick-walled structure of a markedly triangular form, especially when seen from the ventral side (Fig. 14, A), with the apex of the triangle towards the head, where it opens into the truncus arteriosus. Owing to the thick muscular walls the ventricle remains smooth and of about the same size and shape

whether it be empty or distended. It forms the right anterior quarter of the heart, and lies somewhat ventral to the other parts of that organ.

The left auricle or atrium (*L.*) forms the left anterior quarter of the heart, and is its largest division, though on account of its thin distensible walls this chamber may vary considerably in size. Its walls are usually wrinkled and uneven, and its outline is more rounded than that of the ventricle, though the entire outline cannot be seen in either a dorsal or a ventral view, since the chamber is partially covered dorsally by the left auricle, and ventrally by the ventricle. At some point on its dorsal side the vein (*Pul.*) formed by the union of the two pulmonary veins probably enters it, but, on account of the very small size of this single pulmonary vein, its exact point of entrance could not be determined with certainty, and so has not been indicated in the figure. The size of the pulmonary veins in the figure has been exaggerated. The anterior edge of the left auricle lies nearer the head than any other part of the heart except the bulbus arteriosus.

The right auricle (*R. A.*) lies dorsal and posterior to the ventricle and the left auricle, so that in a ventral view of the heart only the posterior half of this chamber shows. Owing to its very thin walls and to the large opening of the sinus venosus it has no very definite shape. It is depressed in a dorso-ventral direction, and its greatest diameter is from side to side. Into its antero-lateral corners open the right and left anterior venæ cavæ (*R. C.*, *L. C.*), while posteriorly it is separated by only a slight constriction, externally, from the sinus venosus which in turn is continued back as the posterior vena cava. Extending longitudinally across the dorsal wall of the right auricle, and closely attached to it, is the pulmonary vein (*Pul.*), formed by the union of the two small veins from the lungs.

The sinus venosus (*S. V.*) is merely the enlarged anterior end of the posterior or inferior vena cava. Its walls are extremely thin, and its size and shape will depend upon the amount of fluid it contains. Blood vessels to supply the walls of the heart may be seen at several places, and are shown in the figure at *R.*

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